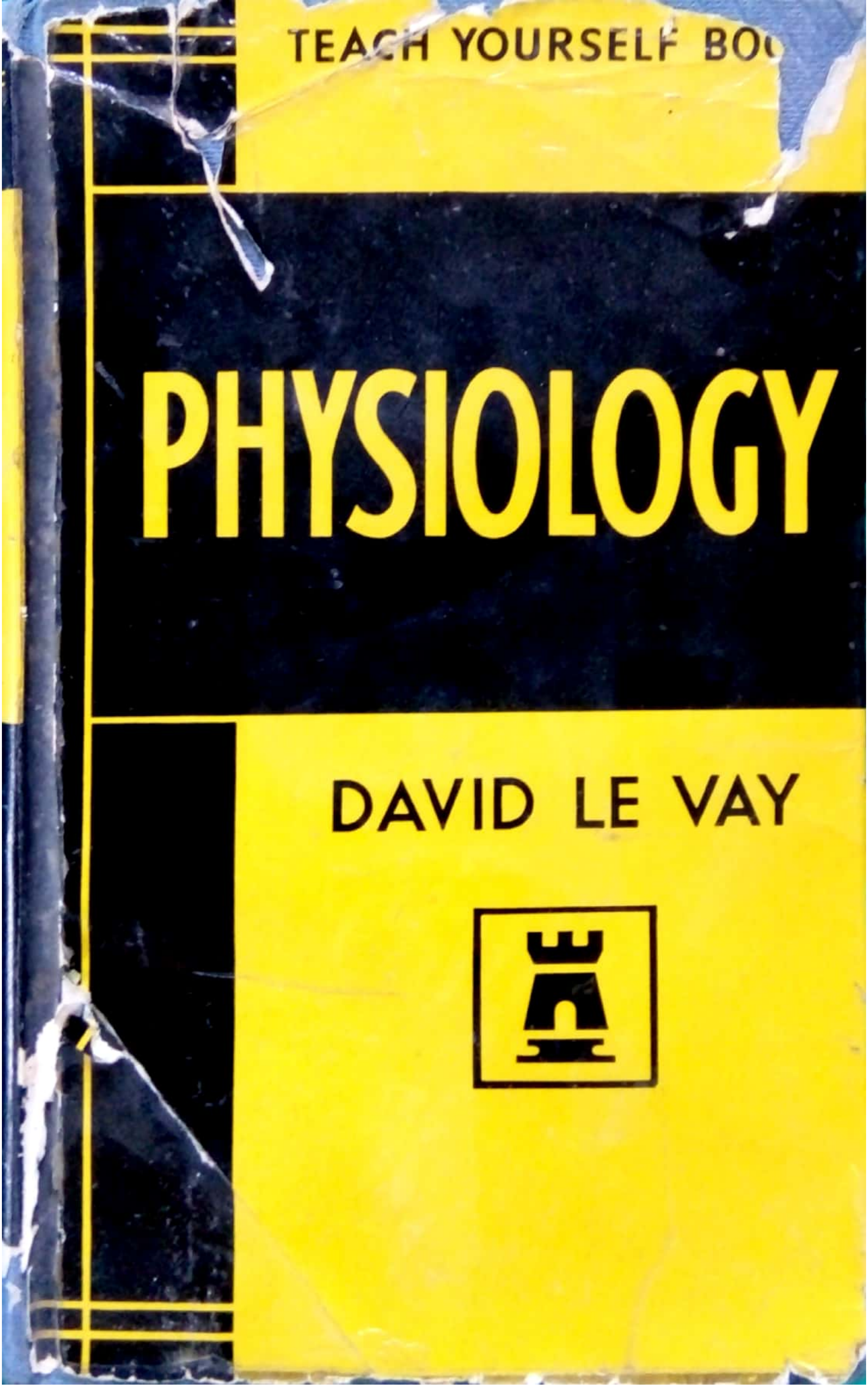

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PHYSIOLOGY

By

DAVID LE VAY
M.S., F.R.C.S.

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PREFACE

THIS simple account of the function of the human body will be found easily within the grasp of all with an elementary knowledge of chemistry and biology. The amount of anatomical information has been kept down to a minimum, but illustrations have been included to make the structural basis of the subject clear. I am indebted for these to Miss Sheila Hayes, of Messrs. E. O. Sonntag, and to Mrs. Lucy Geddes. I am grateful to Messrs. Longmans, Green for permission to redraw certain figures from *Gray's Anatomy* and to Messrs. J. & A. Churchill for the use of illustrations from *Principles of Human Physiology*, and these are individually acknowledged in the text.

D. L.

PREFACE TO SECOND EDITION

IN this edition only minor changes have been made in the text, where these were required in the interests of clarity. The index has been expanded into a Glossary-Index for more convenient reference.

D. L.

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CHAPTER I

WHAT PHYSIOLOGY IS AND HOW IT BEGAN

PHYSIOLOGY is the science of bodily function ; it is concerned with finding out the way in which the living organism works. Thus it is complementary to anatomy, which is the study of the shape and structure of the various parts of the body. Whereas anatomy is an essentially descriptive procedure, physiology is essentially experimental. True, we must describe both the structures and what they appear to do, but to get any further than this, experiment is essential.

Both observation and experiment may be performed on man or animals. Without animal experiments, modern physiology—and for that matter modern medicine—could never have been built up, for animal experiments have the great advantage that isolated organs can be studied. And fortunately the basic working principles of living matter are the same throughout the animal world, whether in microscopic unicellular creatures, or in the myriads of cells of the human body ; and whole organs and systems of organs of other mammals are essentially similar to those of man.

The human body carries on its functions in a constantly changing environment. It is only possible for it to do so if internal standards, e.g., the composition of the body fluids, the degree of aëration of the blood, are maintained at a constant level, whatever the environmental changes. This steady regulation of the internal state, no matter what outer influences affect the body, is an underlying factor of immense importance in physiology, as our subsequent study will show. It can only be achieved because the physical and chemical processes of the body are reversible. The body maintains its internal equilibrium as does a gyroscope, whatever the inclination of the supporting base, until eventually it runs down and topples over in the ultimate irreversible changes of death.

* * *

The history of the growth of physiological knowledge shows how the methods of description, observation and experiment have been applied.

Physiology began with the ancient Greeks. They were often surprisingly accurate in their observations, but were as often misled by speculation, for example on the location in the body of the " vital humours ", and the seat of the emotions and the intelligence. Thus Aristotle in the fourth century B.C. regarded the heart as the organ of reason, but made numerous detailed and accurate records of the development of animals from the embryo. The variations of the pulse were carefully remarked by the physicians of the time, and they were also aware of the difference between arteries and veins ; yet their speculations about the cause of disease were little removed from magic. After the death of Aristotle, the Greek tradition was continued at the school of Alexandria, particularly by Eristratus, who recognized the action of muscles in locomotion and the association of Man's intelligence with the intricacy of the convolutions of the human brain. But he produced a confusing theory, based on the realities of respiration, of the permeation of the blood-vessels and nerves by an essential spirit or *pneuma*, diffused to all organs by the action of the heart.

The greatest figure of physiological antiquity is Galen, who lived in Rome in the second century A.D. ; his writings dominated medical knowledge for over a thousand years, surviving even the Dark Ages, and were restored to Europe in translation from the Arab scholars. Galen described completely the naked-eye structure of the body, though his subjects were apes and not men ; but once again, speculation rather than experiment misled him when it came to postulating function.

The Middle Ages saw the rise of the great Italian universities and medical schools, such as Bologna and Padua, in which regular anatomical dissection of the human body began to produce a firmer basis for the foundation of physiological knowledge. Rather outside their sphere is the great figure of Leonardo da Vinci ; as a brilliant dilettante anatomist, he established the importance of accurate medical illustration and made observations on the actions of muscles and the nature of vision. But he failed to publicize his findings, so it was left to others to remake his discoveries.

In the sixteenth century, Andreas Vesalius, a young Belgian working at Padua, overthrew the traditional reliance on Galen, rejuvenated the medical sciences by asserting the importance of personal observation, and in his masterpiece *On the Fabric of the Human Body* gave the first complete account of human anatomy. He recognized that muscles were stimulated via their nerves, that all muscles had their antagonists which acted reciprocally, and that the arterial pulsation was derived from the heartbeat. He also watched the movements of the lungs in dogs, by removing portions of the ribs. Before Vesalius, the nature of the circulation had been obscured by Galen's insistence that blood passed from one side of the heart to the other through invisible apertures in the intervening partition ; but Vesalius asserted that the septum was impermeable. This resulted first, in the demonstration by Servetus that the transfer of blood is effected through the pulmonary vessels and their ramifications in the lungs ; and second, in the discovery of the nature of the circulation as a whole by the immortal William Harvey.[1]

Harvey was a physician at St. Bartholomew's Hospital, London, and the pioneer of modern experimental physiology. He succeeded in understanding the circulation of the blood, although as yet unable actually to see the capillaries, the fine links connecting arteries and veins, which his theory postulated. His evidence, all of it indirect, was nevertheless conclusive. What clinched the matter was the output of the heart. The heart at each beat must pump about 2 ounces of blood into the aorta, the main artery of the body. The heart beats about 72 times a minute or 4320 times an hour. So over 38 stones of blood leaves the heart every hour, clearly an impossible conception unless there *is* a circulation.

Harvey's methods, combined with the growth of chemical and physical knowledge in the seventeenth century, and the evolution of the microscope, led to rapid advances in physiology. Harvey's assumed capillaries were seen and verified ; blood transfusion in animals was carried out in 1660 (as Pepys noted) ; the red corpuscles of the blood were discovered.

The nature of respiration was made clear by Boyle's demonstration that a part of the air (oxygen) was equally essential to life as to combustion ; inspired air mixed with the blood in the lungs to give it its red arterial colour, deoxygenation in the body as a whole rendered it dark and venous.

A country clergyman, Stephen Hales, stands out in the eighteenth century as one of a long line of distinguished amateur scientists in English life. His greatest achievement was the direct measurement of the blood-pressure in horses, by the use of glass tubes several feet high. Hales' early training was in mathematics and physics, and he was thus able to lay the foundations of our knowledge of the hydrodynamics of the body.

---

[1] Harvey's great book *De Motu Cordis* was published in 1628.

In the latter part of the century the famous surgical brothers William and John Hunter made numerous incidental physiological observations on digestion, the coagulation of the blood, and the growth of bone among others. And the discovery of vitamins was implicit in the Admiralty order of 1795 for the issue of lemon-juice to check the ravages of scurvy in His Majesty's ships. About this time, too, Galvani investigated electrical phenomena within the body and showed that muscles could be made to contract as the result of electrical stimulation.

With the nineteenth century we leave behind the period of slow development by individual effort. The recognition of the single cell as the essential unit of biological structure and function; the discovery of diffusion and osmosis, crystalloids and colloids; the bridging of the gap between inorganic and organic matter by the artificial synthesis of an organic compound, urea, in 1823: all these were of great significance. Furthermore, the conception of metabolism was established—that is, the breaking down of foodstuffs by oxidation within the body to yield carbon dioxide and other waste products, together with the liberation of heat; a process accompanied by as exact an equivalence of energy interchange as any reaction carried out in a crucible, and no less subject to the laws of thermodynamics.

A picturesque episode is that of Beaumont in America, studying gastric function in Alexis St. Martin, a trapper shot in the abdomen. As a result, St. Martin had developed a permanent opening or fistula between the stomach and the surface of the abdomen. This allowed Dr. Beaumont to carry out for the first time the direct observation of the reactions of the stomach to various foodstuffs, as shown by the flow of secretion and changes in motility.

It is to a Frenchman, Claude Bernard, that we owe the idea of the constancy of the internal environment, upon which the relatively independent life of man depends. His conception was that of a mechanism always acting so as to neutralize the effects of any change in external environment, maintaining an internal equilibrium in which all cells and fluids remain unchanged in essential properties ; a regulation achieved by the diffusion of water, oxygen, food and heat through the vascular system, the whole co-ordinated and modified by the nervous system. In this regulation, the glands of internal secretion, the endocrine organs such as the thyroid, were shown to have an important role.

Finally there has been the development of our knowledge of the nervous system. Sir Charles Sherrington, at Oxford, demonstrated the self-regulating nature of bodily posture and the activities appropriate to the different levels of the brain. I. P. Pavlov demonstrated clear links between mind and body by his study of conditioned reflexes—that is, bodily responses produced by the brain reacting, not to the original stimuli, but to others it has learned to associate with them. Indeed, Pavlov went so far as to suggest that human behaviour might be considered as a mass of such reflexes. More recently still, the psychologists have entered the field of physiology, by demonstrating the immense influence of the emotions and unconscious life in general on the most basic of physiological activities, such as the heartbeat and digestion.

CHAPTER II

THE ANATOMICAL BASIS OF PHYSIOLOGY

THE unit of living tissue is the microscopic *cell*, having its own capacity for life. The body is composed of different *tissues*, each of which is an aggregation of the same kind of cell, together with a certain amount of intercellular substance between the cells. In addition, there is much material produced by cellular activity,

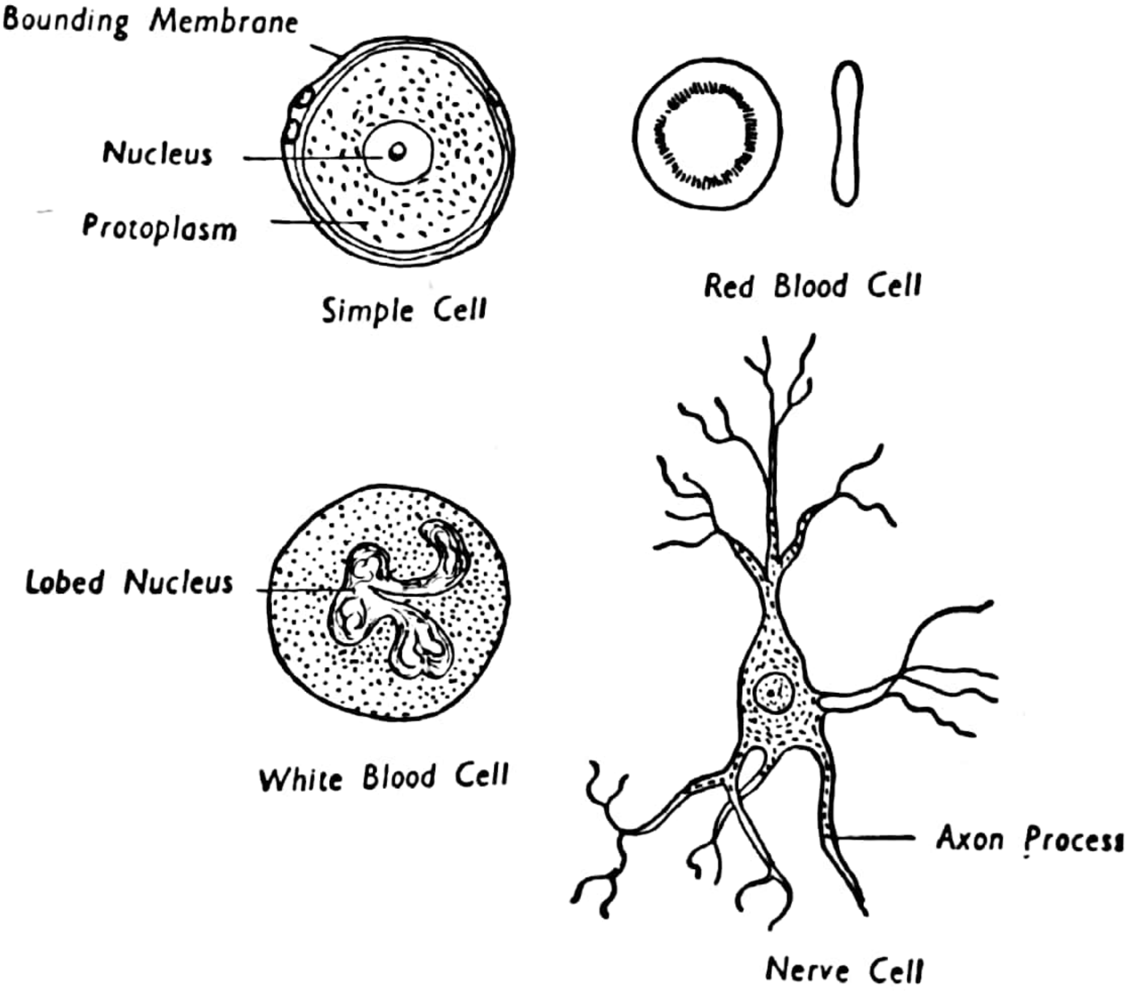


FIG. 1.—Various types of cell.

but no longer living, e.g., the mineral content of bone, the hair and nails.

The essential parts of any cell are the *bounding membrane*, the *protoplasmic substance*, and the *nucleus*, itself a denser mass of protoplasm in the centre. All the cells of the body have sprung from the division of the female germ cell (the *ovum*) after its fertilization by the male germ cell (the *spermatozoön*). In order to ensure an exactly equal sharing to the new cells, as they are formed, of the *genes*—the factors of inheritance contained in the nucleus—cell-division is an extremely complicated process. This process is described as *mitosis* ; within the nucleus a group of rod-like *chromosomes*, which carry the genes like beads on a string, split up to be divided between the two daughter cells. Occasionally a cell and its nucleus just break into two, but this is uncommon.

The cells of different tissue may be greatly modified in their specialized functions, e.g., the red cell of the blood has lost its nucleus, the nerve cell has an enormously elongated axon-process to carry stimuli, the striated muscle cell possesses the capacity to contract in length. But despite these modifications, in each case the essential components remain recognizable. There are only four essential tissues—*epithelium*, *connective* tissue, *muscle* tissue and *nervous* tissue ; though each of these may be further modified in various ways. They differ in the nature of their component cells, and in the particular kind of secreted intercellular substance, the cell background or *matrix*.

1. Epithelium. This covers all free body surfaces, not only the external surface of the skin, but also the internal surfaces which line the body cavities. It also provides the linings of the vessels, and of the respiratory, digestive and urinary tracts ; and of the glands opening into them. It is important to realize that both internal and external surfaces of the body possess this intact epithelial envelope ; it is normally unbreached, and stands as a barrier between the outside world (including, paradoxically, the contents of the bowel and hollow organs) and the deeper muscular, connective and nervous substance of the body. These inner and outer linings blend with each other at the orifices of the various cavities—at the lips, anus, nose and urethral aperture, where the linings of digestive, respiratory and urinary tracts become continuous with the skin. Epithelium is typically very cellular and simple in arrangement, with little ground substance and no blood vessels of its own. The cells are arranged in a single mosaic layer, or in row on row. And most of the pigment of the body is found in this tissue, in the skin, iris and retina.

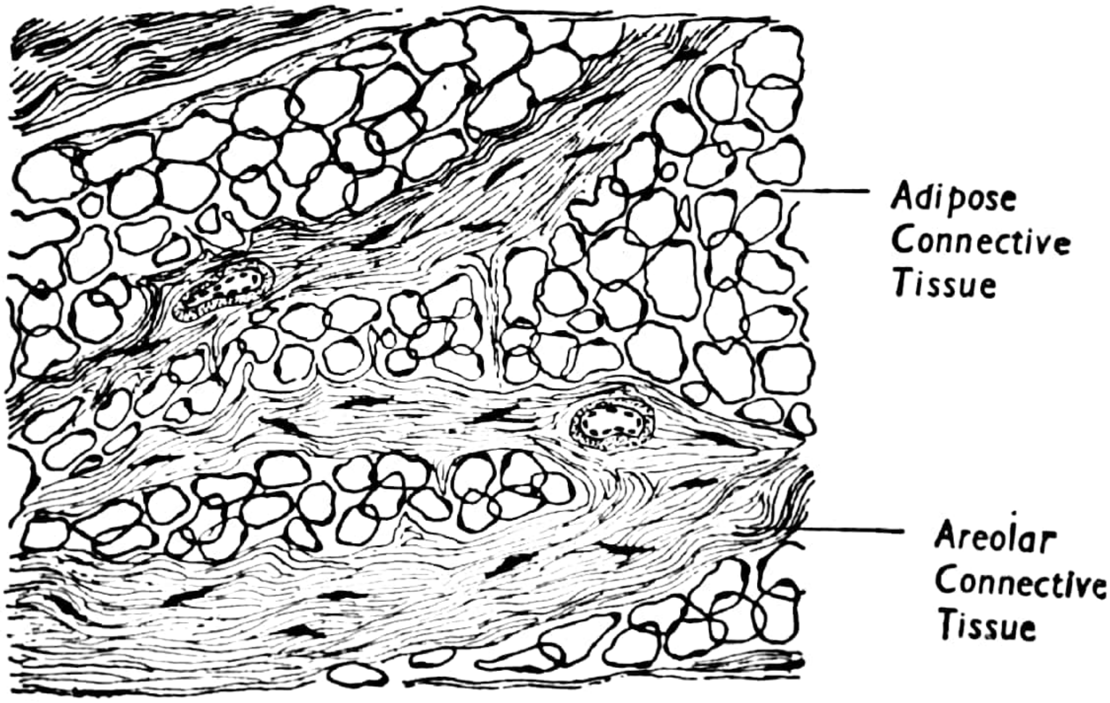


FIG. 2.—A simple connective tissue.

2. Connective Tissue in its various forms is the supporting framework of the body as a whole, and of each organ in particular. It has a large amount of intercellular matrix, and the exact nature of a connective tissue depends on the particular qualities of this matrix and of the fibres it may contain.

Thus, in simple *areolar* tissue, the loose packing in clefts and spaces which also separates the skin from deeper layers, there is a semifluid matrix containing white (unyielding) and yellow (elastic) fibres, an arrangement allowing gliding of part on part. Predominance of fibres produces either strong non-elastic *white fibrous tissue* of tendons and ligaments, or the resilient *elastic tissue* of the arteries and spinal ligaments.

In *adipose* tissue, found everywhere except within the skull cavity, the cells are modified to carry fat globules.

In *blood* and *lymph*, the matrix is completely fluid, while the cells have become modified either to carry dissolved respiratory gases or to deal with invading micro-organisms.

In *cartilage* and *bone* the matrix has become hard and solid by impregnation with mineral salts.

Cartilage is a gristly tissue without blood vessels, and forms the joint surfaces, the framework of the air-passages, etc. Thus it occurs where rigidity and resilience are needed in combination. In the developing embryo, the skeleton is entirely cartilaginous at one time, this being slowly replaced by bone.

Bone itself is an intimate blending of organic fibro-cellular substance and inorganic mineral salts—calcium phosphate and carbonate, magnesium and fluorides. The organic part consists of fibrous tissue containing numerous cells called bone corpuscles or *osteoblasts.* The matrix is impregnated with mineral matter. The organic part can be removed by burning, leaving a brittle mineral skeleton. The inorganic matter is readily dissolved by acid, the decalcified bone being then perfectly flexible. The *periosteum* is the tough membrane surrounding the bone ; its outer layer is purely supporting, but on its deep aspect there are bone-forming cells responsible for the increase in girth of the bone during growth. Bone receives its blood vessels via the periosteum and depends largely for its nutrition on the latter's integrity ; if, for example, the membrane is stripped up by inflammatory exudate, much of the shaft may die.

The general *functions of bone* are the provision of framework and support for the body, points of attachment for muscles, the protection of internal organs, and finally the formation of the cells of the blood in the bone-marrow. In the ordinary long bone of the limbs there is a roughly cylindrical shaft and two expanded ends ; sometimes an end is rounded off as a head, or widened into pulley-like condylar masses. These ends take part in formation of the adjacent joints, and are covered with smooth articular cartilage to facilitate movement, the two surfaces concerned being enclosed in a common joint capsule ; thus the periosteum covering the shaft of the bone becomes continuous with the joint capsule at the end of the bone.

Cross-section of the shaft reveals an outer *cortex* of hard bone and a central medulla or marrow cavity ; at the ends, however, there is no cavity but a solid mass of spongy bone. Yellow fatty marrow occupies the cavity in the adult and the meshwork of spongy bone at the ends is filled with red marrow ; this red marrow is responsible for the production of red and white blood corpuscles.

In the early years of life, red marrow occupies the whole shaft, but retreats to the ends with growth ; and this process can be reversed in later life if necessary, as in chronic anaemia, when the shafts are permanently occupied with red marrow working overtime to satisfy

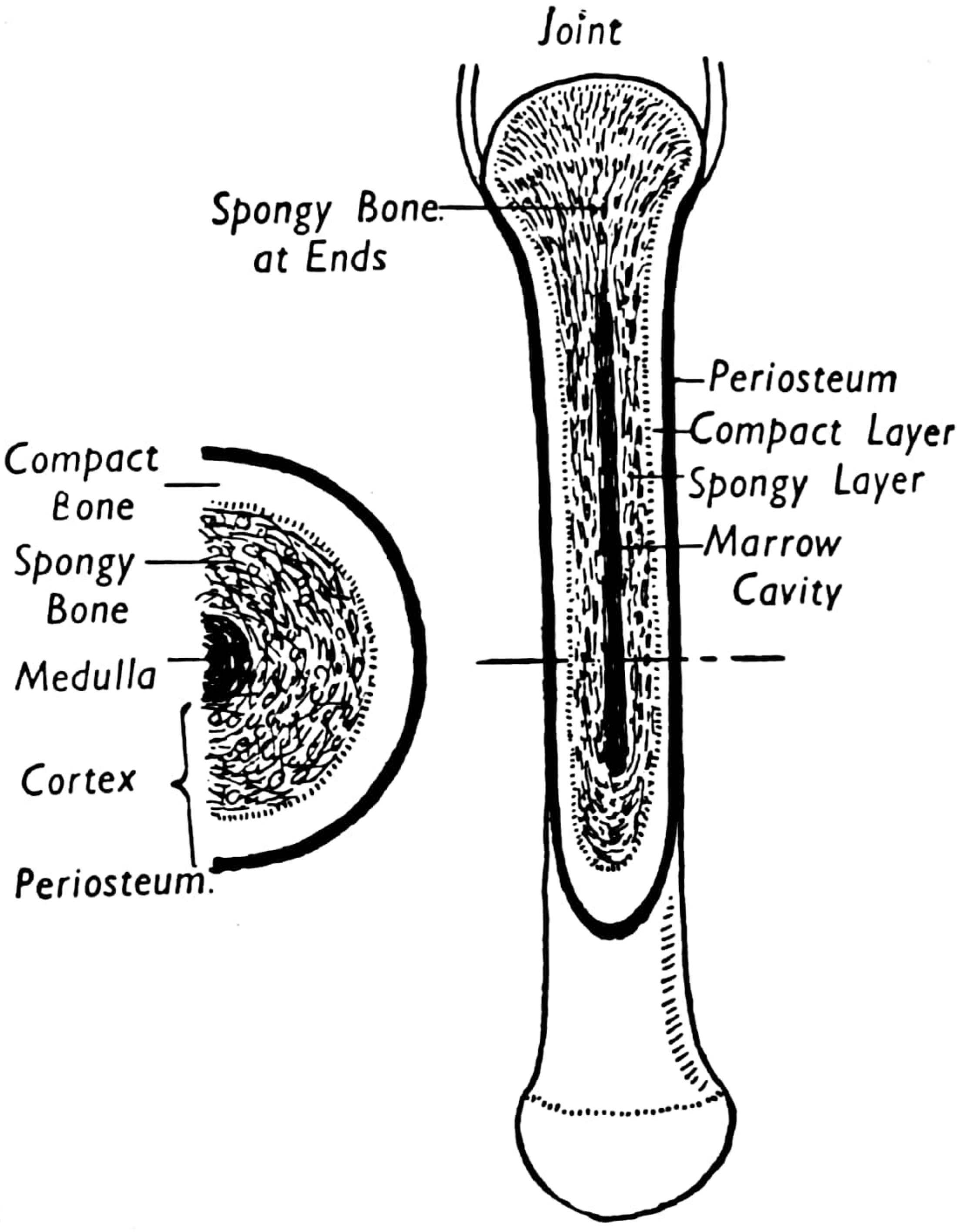


FIG. 3.
(*a*) Cross-section of a long bone.
(*b*) Longitudinal section of a long bone.

the demands of a system short of blood. The short bones of the spine and flat bones such as the breast-bone, ribs and skull, are always filled with red marrow as they have no medullary cavity.

Growth of Bone. Mammals are peculiar in the animal world for the relatively long period of growth before maturity is reached, a process associated with the evolution of higher mental processes. One consequence of this is that growth of the skeleton continues until 18 to 20 years of age. To permit this continued growth in length, the long bones have growing-ends, or *epiphyses.* At birth, the shafts are entirely ossified (bony), but the ends are still cartilaginous ; in the first years of life, separate secondary centres of ossification appear in the ends, which then ossify completely, except where a thin cartilaginous plate separates them from the shaft. The bony end is called the epiphysis, and the cartilaginous plate its epiphyseal plate. The plate consists of columns of cartilage cells, continuously reproducing themselves on the shaft side of the plate, and as continually turning into new bone which is pushed away into the main shaft, enabling it to grow in length. The epiphyseal plate retains its integrity, until the epiphysis fuses with the shaft at maturity by ossifying across the intervening cartilage ; at 16 to 18 in men, 14 to 16 in women.

Complete destruction of an epiphysis causes cessation of growth ; partial destruction by injury or disease causes a distortion of growth, in which the limb turns away from the still active side.

There is an intimate relationship between bone growth, including the chemistry of the minerals of bone, and certain endocrine or ductless glands. Excessive secretion of the pituitary gland at the base of the brain in childhood so stimulates epiphyseal growth as to cause gigantism ; the action in the adult is less spectacular, but even here gross hypertrophy of the bones of the hands, feet, and jaw results. In congenital deficiency of the thyroid gland (cretinism) the reverse situation arises, with a combination of idiocy and stunting; the epiphyses are delayed in appearance and still unfused in middle life.

The amount of vitamin D in the diet also plays a part in bone chemistry. Infantile rickets, the result of vitamin D deficiency, produces its deformities partly by rarefaction and consequent softening of the shafts, and partly by disturbing epiphyseal ossification. Vitamin D acts by regulating the interchange between the calcium and phosphorus dissolved in the blood and the calcium phosphate of bone. A further factor in this regulation is the secretion of certain small glands near the thyroid gland in the neck, the parathyroid glands, overaction of which causes general brittleness of the skeleton, with deformity and spontaneous fracture.

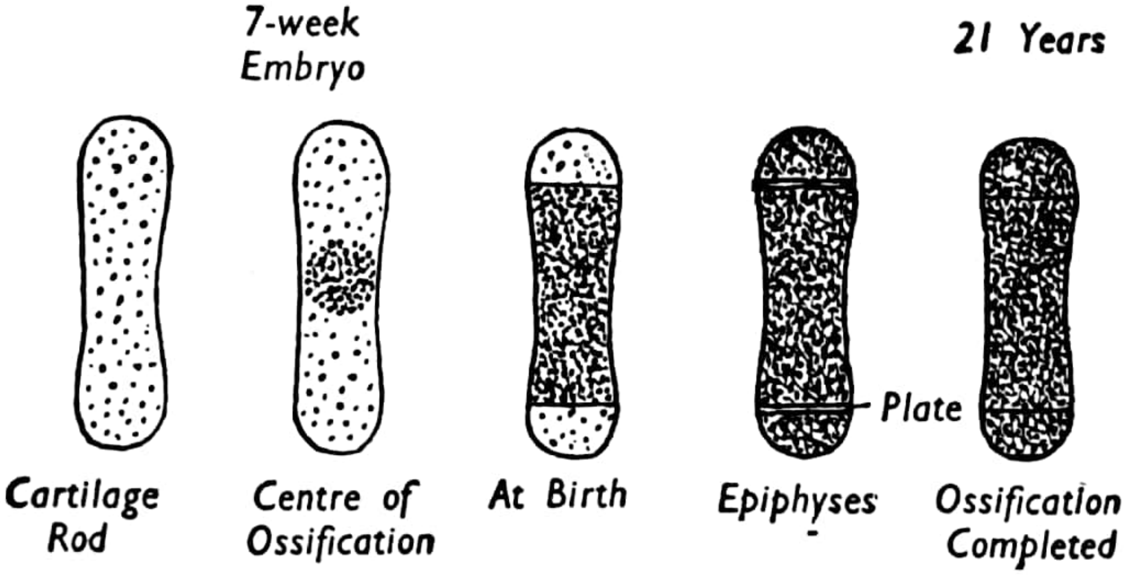


FIG. 4.—Stages in the ossification of a long bone.

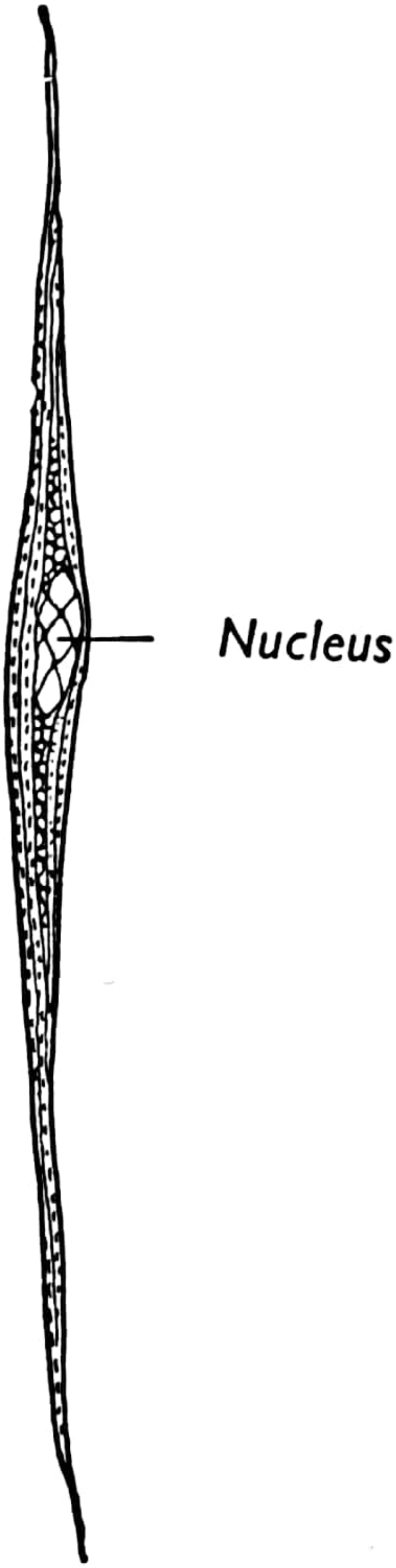
The hard bones of the dried skeleton hide from us their essential plasticity in life, for they respond to stress much as a tree responds slowly to the deforming influence of wind and weather. They hypertrophy in response to extra loads, particularly if this takes the form of longitudinal compression; the internal arrangement of bone strands or trabeculae is a purely mechanical solution to the problems stresses impose on them. In view of this exact correspondence between form and functional needs, it is remarkable to find an inherent tendency to assume the adult shape, even in a bone removed from the embryo and left to develop entirely isolated in an artificial culture medium contained in a flask.

3. **Muscular Tissue** is composed of reddish muscle fibres, arranged in bundles which are bound together by areolar tissue. These fibres are themselves composed of highly specialized and greatly elongated cells characterized by their power of *contraction*, or shortening on stimulation. This power of shortening on stimulation is an exaggeration of a property inherent in some measure in all protoplasm, even in simple unicellular animals.

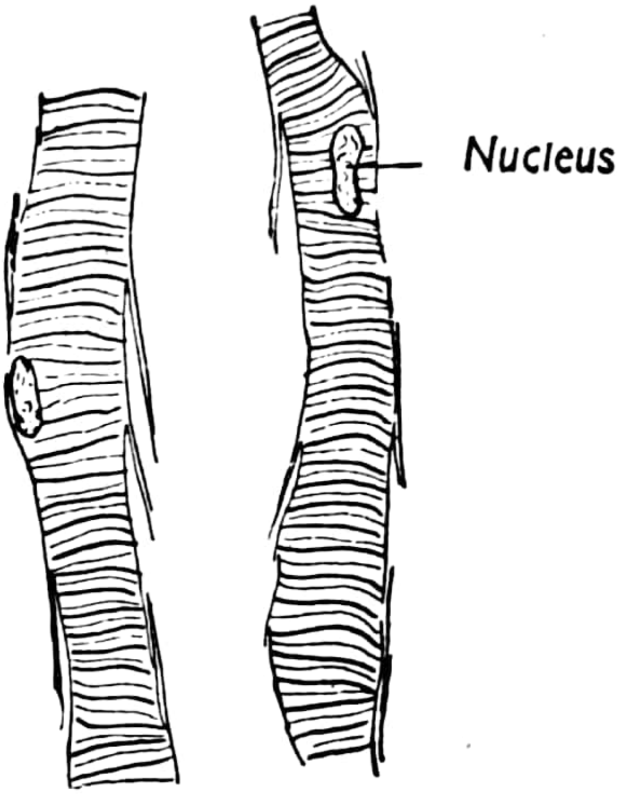
There are three types of muscular tissue associated with different minute structure and fulfilling differing functions (Fig. 5):

(i) *Smooth* or plain muscle (unstriped, involuntary or visceral) is the most primitive and least specialized type. It forms the contractible layer of the blood vessels and the viscera—the hollow internal organs. All these structures work automatically and unconsciously without the interference or knowledge of the brain, being regulated by the semi-independent autonomic or vegetative nervous system.

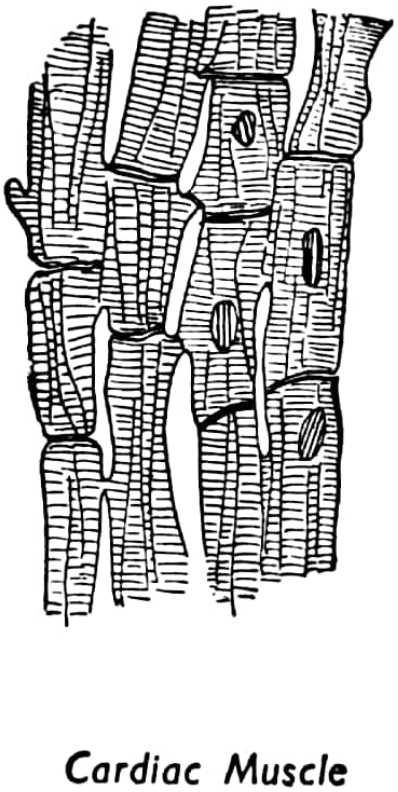
(ii) *Striped* muscle (skeletal, voluntary) has more intricate fibres which are seen to be striped or cross-striated under the microscope; they are found in the muscles attached to the skeleton—the muscles of the



(*a*) A smooth muscle fibre.



(*b*) Striped muscle fibres (after *Gray*).



(*c*)

FIG. 5.—The three kinds of muscle fibres.

limbs and trunk. They are under the conscious control of the central nervous system.

(iii) *Cardiac* muscle, the substance of the walls of the heart, occupies an intermediate position. Its fibres are striped, though their action is not under voluntary control. Unlike the other two types, the fibres are branched and there is no clear demarcation between individual muscle cells.

4. **Nervous Tissue** is characterized by the sensitivity of its cells to stimuli and by the great conductivity of the fibres arising from these cells. This sensitivity and conductivity are again exaggerations of a property possessed by all protoplasm—*irritability*. Each nerve cell has several branching processes or *dendrites* interlocking with those of adjacent cells ; and one process is elongated as the main *axom* for transmission of stimuli ; often this is enormously long, traversing the length of the limbs or spinal cord. Cell, dendrites and axon constitute the nerve unit or *neurone* ; and the nervous system is built up of millions of such units in close and complex interrelation.

Nerve fibres are grouped in bundles, both within the brain and spinal cord, and outside the central nervous system where they are gathered into nerve trunks. There are two kinds of nerve fibres. The larger white, or *medullated*, fibres have a fatty sheath to insulate their electrical charges, and are found in the central nervous system and the main nerve trunks. In the part of the nervous system controlling unconscious internal processes, the autonomic system, the fibres lack this fatty sheath and are therefore grey in colour and are spoken of as *non-medullated*. Damage to nervous tissue is irreparable in so far as the cells are incapable of reproduction ; but the function of destroyed areas in the cerebral cortex may sometimes be assumed by other parts of the brain. Injured fibres may, however, grow again, but even then only in the peripheral nerves and never within the brain or spinal cord.

* * *

So much for the tissues of the body. A word must now be said about their general arrangement.

Body Wall and Body Contents. The body wall or *parietes* encloses the great cavities, the abdomen

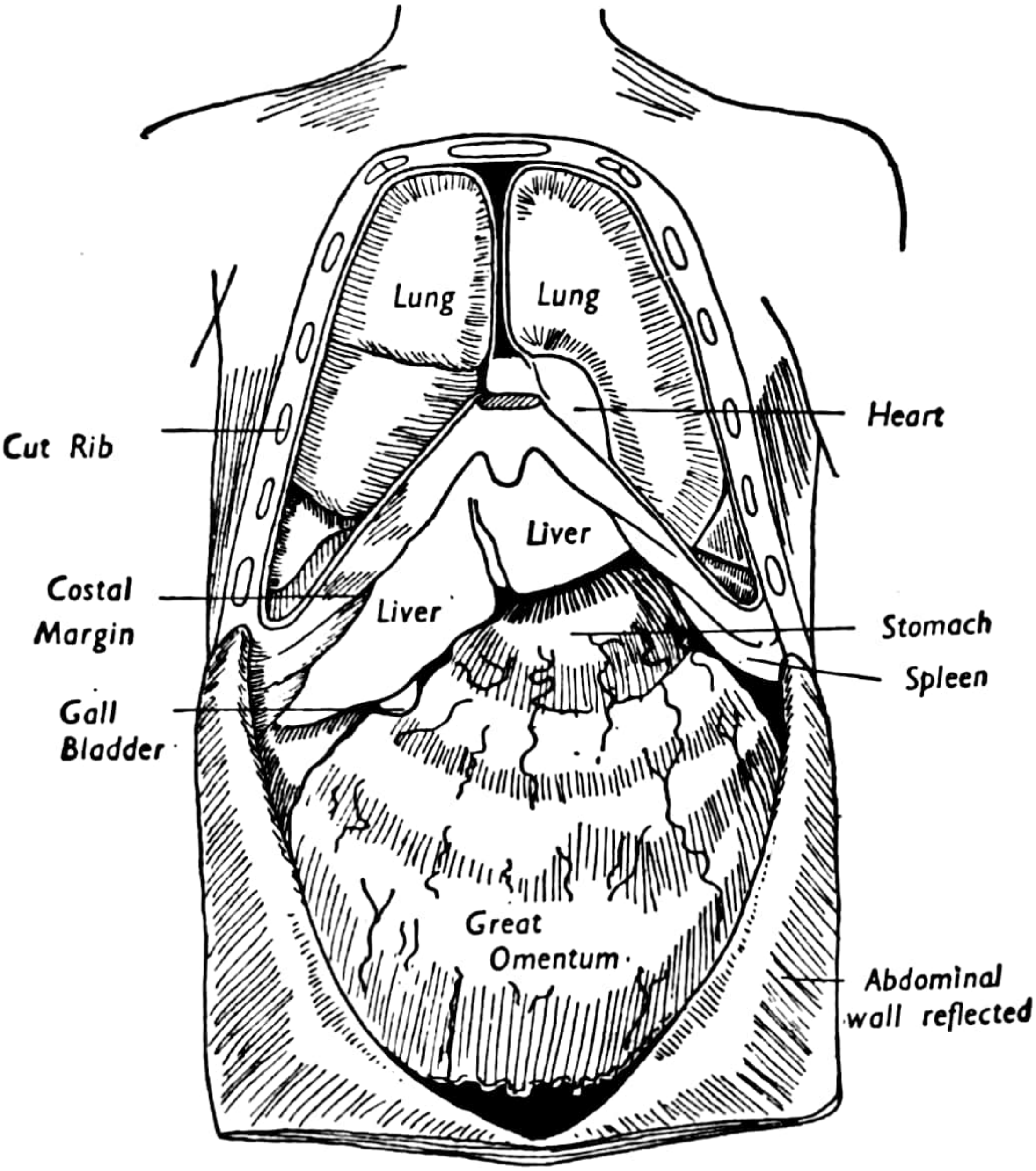


FIG 6.—The viscera exposed by removal of the anterior walls of abdomen and thorax.

and thorax; these are also named after their lining membranes—as the *peritoneal* and *pleural* spaces. Essentially, the body wall is composed of the skeleton with its attached muscles and connective tissues, and the overlying skin and fat; these are termed the *somatic* structures.

The cavities, with their smooth serous linings, contain the internal or *splanchnic* organs, the *viscera*; these are lungs and heart in the chest, the stomach, intestines, and various glands and other organs in the abdomen. They develop in the embryo from the back of the body wall and retain this attachment in the adult, the lungs by their roots, the intestine by its supporting membrane or mesentery. And we have already noted that the parietal skeletal muscles are under the control of the will, while those of the viscera function unconsciously and automatically.

The Body Systems. These are described fully in their respective chapters. They are as follows:

1. The *skeletal system*, the bones.
2. The joints or *articulations*.
3. The *muscles*

Together constituting the *locomotor system*.

4. The *respiratory system*.
5. The *digestive system*.
6. The *urogenital system*.

Together constituting the *viscera*.

7. The *vascular* or circulatory system—heart, blood vessels, lymphatics.
8. The *nervous system* and special sense organs.

CHAPTER III

THE BIOPHYSICAL BASIS OF PHYSIOLOGY

WATER is the universal fluid medium of the body. It provides the means of transport inside the body of food, wastes and respiratory gases ; and its properties allow these to diffuse into and out of the cells. Water constitutes up to 95 per cent of cell protoplasm and 70 per cent of the body weight, and no chemical substance can influence the behaviour of the living cells until it is first brought into solution.

Thus, from the physical angle, the essence of bodily function is concerned with the behaviour of molecules in watery or aqueous solution. The ordinary laws of physics apply to such solutions. Thus, by diffusion, the salts in the blood or the sugar in the cerebrospinal fluid are uniformly concentrated, and the amount of these substances in solution is the same wherever we take our sample.

Certain membranes allow water and dissolved substances to pass freely through them ; if such a membrane separates two solutions of different strength, their concentration is ultimately equalized by the transfer of water and solute (substance dissolved) in reverse directions. This physical process is called *dialysis*. Membranes vary in the size of the molecules they will allow to pass, and most of the cell-membranes of the body are only semi-permeable ; such membranes allow a free passage to water, but are permeable only to some dissolved substances. If such a semi-permeable membrane separates two solutions, the one stronger than the other, of a substance which cannot traverse the membrane, water is drawn through the membrane from the weaker to the stronger side, and this attraction of water is known as *osmosis* ; and the *osmotic pressure* of the solution is the expression of the energy gradient set up by the tendency of water always so to dialyse as to dilute the stronger solution. Thus, a pig's bladder filled with strong sugar solution, when immersed in water or in a weaker sugar solution, attracts water in and swells up.

The behaviour of living cells in the body, whether aggregated in the tissues or freely floating in the blood, is intimately affected by the relative osmotic pressures of the surrounding medium and of the cell substance itself. The intervening cell-membrane is semi-permeable, and may be compared with the pig's bladder in the experiment quoted. Thus, a red blood cell, immersed in strong salt solution, shrivels up as water is sucked out of it ; but it swells up and bursts in a weaker solution or in water.

There is obviously an intermediate osmotic pressure for the surrounding medium which is identical with that of the cell protoplasm ; a solution of such an osmotic pressure leaves the cell unaffected, and it is known as an *isotonic* solution. The stability of behaviour of the body cells is such that all their osmotic pressures are identical and isotonic with a 0·9 per cent solution of common salt (sodium chloride) ; and this is spoken of as " normal saline ". Normal saline is thus identical osmotically with the blood and lymph, and is used experimentally to bathe cells and tissues without harming them.

Whatever the substances concerned, solutions containing the same number of molecules per unit volume have the same osmotic pressure. And therefore solutions of different substances of the same *percentage* strength have osmotic pressures inversely proportional to the sizes of their molecules or molecular weights ; i.e., a 1 per cent solution of protein, which has enormously large and complex molecules, contains far fewer particles per cubic centimetre than a 1 per cent solution of sugar, and its osmotic pressure is correspondingly less. Furthermore, certain substances called electrolytes *ionize* in solution ; that is to say, their molecules split or dissociate into two or more electrically charged ions. The osmotic pressure of these solutions is greater than would be expected from the size of the molecules, for it is proportional to the total concentration of *particles* present.

Solutions have a further property of great physiological importance, resulting from this tendency of some substances to ionize. This property is their chemical *reaction*, whether acid, neutral or alkaline. Acidity is due to the presence of hydrogen ions ($H^{\cdot}$) and alkalinity to hydroxyl ions (OH') ; the reaction of water is neutral because when it dissociates it produces these ions in equal amounts. In any solution, the product of hydrogen and hydroxyl ion concentration is constant, so that they are inversely proportional to each other. For this reason the acidity or alkalinity of a solution can be estimated by measuring its *hydrogen-ion concentration* alone. This is always a small figure (a litre of water contains only 10^{-7} grammes of hydrogen ions) and it is therefore customary to use the power of 10 as a positive number—the hydrogen-ion exponent or pH.

Thus the pH of water is 7, and this is the central point of chemical neutrality ; the pH of a solution falls as its acidity rises and increases as it becomes alkaline, a single step such as from pH 7 to 8 indicating a tenfold increase of alkalinity. The reaction of the blood is constantly just on the alkaline side of neutrality, at pH 7·4. Cell functions are profoundly modified by small changes in chemical reaction ; only a small increase in acidity or alkalinity suffices to suppress their activities—for example to bring such an organ as the heart to a stop. Nevertheless, small amounts of acid and alkali are constantly being formed in cellular life, and their effects are minimized by certain " buffer salts " in the body fluids and cell protoplasm which take them up automatically and prevent any change in the general reaction. The main buffer of the body fluids is sodium phosphate, and that of the cells is sodium bicarbonate, each of which can so vary between its own acid and alkaline forms as to compensate for any change in the reaction of the medium ; and proteins themselves can function either as weak acids or bases, and can therefore absorb either so as to stabilize the pH of the cells they compose.

Crystalloids and Colloids. All substances fall in two classes : *crystalloids*, simple crystallizable compounds like sugar and salt, which diffuse easily in water and traverse animal membranes ; and *colloids*, complex materials like gelatin and egg-white which crystallize with difficulty or not at all, diffuse slowly, and cannot cross membranes. Obviously the two can be separated by the process of dialysis already referred to, and the essential difference between the classes lies in the size of their molecules ; the molecular weight of salt is 58·5, while that of proteins is of the order of 100,000.

Colloids may exist either as *sols* in apparent solution ; or as *gels*, a solid jelly state with water. In fact, colloidal solutions are really only suspensions of particles, a disperse phase in the continuous phase of some fluid medium. These so-called phases are reversible, as when milk, a suspension of oil in water, becomes butter, a suspension of water in oil.

One feature of colloidal " solutions " is that their surface layer has a much greater concentration of the colloid substance than the mass of the solution ; and this is the basis of the formation of the bounding membrane of living cells, the membrane whose semi-permeability is responsible for the osmotic transfers already discussed. This membrane is also responsible for maintaining certain differences between the contained protoplasm and the surrounding medium.

Thus there is constantly more potassium than sodium in red blood cells, though the reverse is the case in the plasma itself, the fluid component of the blood. And again, most cells have a slightly acid reaction of pH 6·8, although immersed in neutral or slightly alkaline surrounding media. These differences are maintained by the selective action of the cell membrane ; but this selective action is not purely physical, for the outer layer contains fatty materials and can therefore be penetrated by chemical agents soluble in fats, such as ether and alcohol ; such substances act as anaesthetics by influencing the brain cells in this way, and they will also kill individual cells on direct application. Colloidal solutions are unstable and the suspended particles may be precipitated by heat, by changes in reaction or the addition of salts ; the *coagulation* of protein sols produced by heat is familiar to us in the case of the albumin of egg-white. A further important property of colloids in relation to their behaviour in living matter is their enormous power of *adsorption* of other substances due to the immense surface area presented by the dispersed particles. Adsorption is the capacity to pick up and retain a substance, without entering into chemical combination with it.

We may now review the basic physical factors which control the transference of substances across cell membranes. These are :

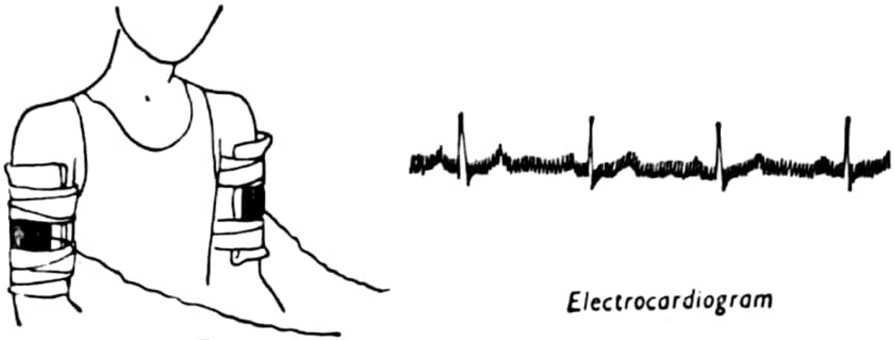
(i) A difference of *hydrostatic pressure* between the two sides, i.e., the difference in pressure between two unequal columns of water, connected at their lower ends. Thus, when excess water is eliminated from the blood via the kidneys, the osmotic pressure of the proteins dissolved in the blood plasma resists its outward passage from the capillaries into the kidney tubules. This osmotic pressure is the equivalent of 30 mm. of mercury. However, this is normally overcome by the hydrostatic effect of the blood-pressure—say 130 mm. of mercury—which drives the water across. But if the blood-pressure falls below 30 mm. because of disease or shock, urine ceases to be formed.

(ii) The ordinary laws of *diffusion* and *osmosis*, depending on the relative strengths of the solutions on either side.

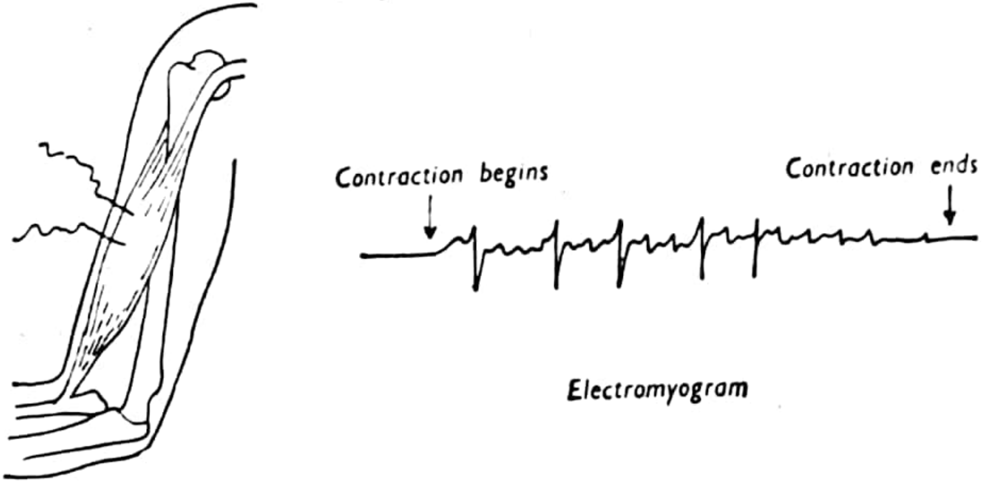
(iii) Differences of *electric potential*.

(iv) The varying *permeabilities* of the membranes themselves. Only rarely are they absolutely impermeable; and none are completely semi-permeable, i.e., none allow the passage of water only. Some allow crystalloids, certain colloids and water to cross, but the usual semi-permeable variety permits water and crystalloids only. In certain cases substances will only pass in one direction, due to changes they produce in the membrane. A final point is that, in the dialysis of a compound of one diffusible and one non-diffusible ion, a difference of chemical reaction develops between the solutions on the two sides of the membrane; this phenomenon provides the basis for the secretion of the highly acid and alkaline digestive juices of the stomach and pancreas respectively.

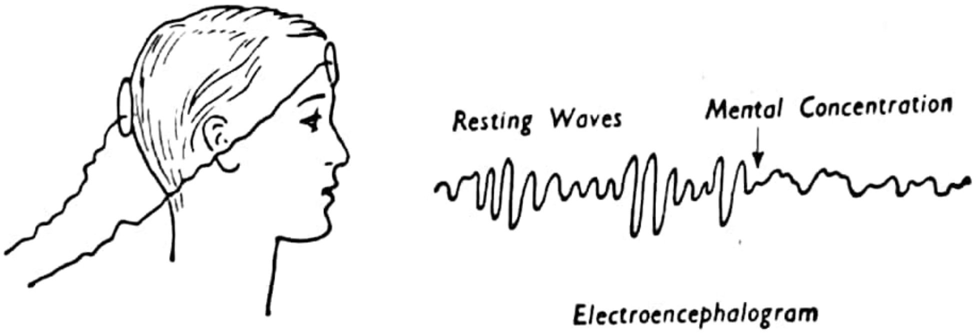
Body Electricity. Living cells are permeated by electrolytes dissolved in water, and these are dissociated in varying degree into electrically-charged ions which will carry a current through the tissue. Furthermore, cell protoplasm contains colloidal particles, also often charged, which may be non-diffusible and so bind the simpler ions as to set up a difference of electric potential (and of chemical reaction) on two sides of a membrane. As a result, all functional changes in the tissues produce changes in electric potential—whether these changes be the heartbeat, glandular secretion, muscle contraction, or the intimate activities of the single cell itself.



Electrocardiogram



Electromyogram



Electroencephalogram

FIG. 7.

As far as the heart, brain and muscle are concerned, it is an everyday matter in medical practice to record these changes and their alteration by disease (Fig. 7).

Thus the *electro-cardiogram* is a record of the heart's electrical activity. It is obtained by attaching wires to the body in certain conventional positions. The electrical currents are transmitted through the chest wall to the limbs, where they are picked up by electrodes and carried to a string galvanometer or a cathode-ray recorder. The impulses are recorded photographically, and the changes seen on the chart are due to contractions of different parts of the heart in succession; a cycle repeated over and over again.

The *electro-myogram* is obtained by the actual insertion of a needle electrode into muscle; there is an absence of changes with complete relaxation, but contraction sets up a storm of electrical impulses which gradually die away again.

Lastly, the *electro-encephalogram* is a similar record of rhythmical electrical discharges from the brain, obtained by using scalp electrodes. There is a spontaneous rhythm of discharge which is modified by mental activity and by the receipt of sensations such as sound and light; and this is grossly distorted by any tumour of the brain, which produces a "silent" area.

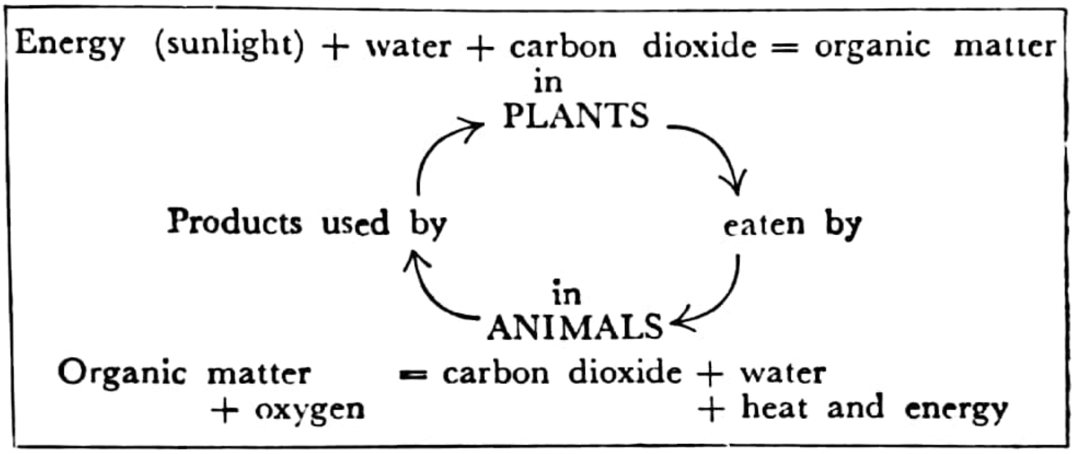
CHAPTER IV

THE BIOCHEMICAL BASIS OF PHYSIOLOGY

THE essential chemical elements of protoplasm are carbon, hydrogen, oxygen, nitrogen, sulphur and phosphorus. Simple compounds of these such as water and carbon dioxide require an elaborate synthesis for their conversion into organic or living matter ; this is effected by green plants under the influence of sunlight. Neither man nor animals can achieve this synthesis for themselves ; they are dependent on the consumption of vegetable matter directly, or indirectly, after it has been utilized by other animals which serve as food in their turn. In the final processes of digestion and absorption, the constituents of the food are temporarily broken down into simpler organic substances which are reassembled in the tissues of the body in a manner which is never quite the same for different animal species. The finished products—subcutaneous fat, heart muscle and so on—differ slightly in chemical composition as between man and animals.

Man, then, depends for body building material and sources of energy on the complex organic compounds, the carbohydrates, fats and proteins, which have been built up in living plants. Oxygen is of special importance as the only chemical element he takes up as such in its free state—in the inspired air (though it is also used in combination). Oxygen frees the potential energy of the foodstuffs by burning or oxidizing them in the cells of the body to form carbon dioxide and water, and at the same time liberates energy.

This last step is therefore the complete reversal of what the green plant has originally achieved. Since the breakdown products of animal tissues are used again by plants, there is a continuous cycle. On this cycle both animals and plants depend. Thus the energy for our body heat and movement has been ultimately derived from the sun.


Energy (sunlight) + water + carbon dioxide = organic matter
in
PLANTS
Products used by
eaten by
in
ANIMALS
Organic matter + oxygen = carbon dioxide + water + heat and energy

This cycle is concerned with carbon, hydrogen and oxygen only ; but similar cycles apply to the other essential elements of the food such as nitrogen. This is mainly synthesized into organic matter by minute plants, the soil bacteria, on which the plant kingdom as a whole is dependent ; then the plants pass it on to man and animals ; and these return it in the urea and ammonia of their excreta to be used in the soil again.

A number of substances are also essential to the body, but are taken in in the form of simple mineral salts. Thus potassium, sodium, calcium, magnesium, chlorine and phosphorus are taken in as sodium chloride, calcium phosphate, etc. Iron is a special instance of a mineral essential to life, for it is an essential part of the red pigment of the blood, haemoglobin, which is responsible for the transference of oxygen from the lungs to the tissues.

Lastly, there is a group of what are known as *trace* *elements*, essential though needed in very small quantity only. These include iodine, a constituent of the secretion of the thyroid gland ; fluorine, necessary for proper hardening of the enamel of the teeth ; copper, complete deprivation of which is a cause of anaemia ; and manganese. Do not confuse these with the vitamins, which are complex chemical compounds to which we shall refer later.

Complex though the varieties of living matter and of foodstuffs appear, they can be grouped into three great classes of compounds. These are the *fats*, *carbohydrates* and *proteins*.

The *fats* occur in the adipose tissue found beneath the skin and elsewhere, and as discrete globules in the cells everywhere, particularly in the liver. They are essentially combinations of glycerol (or glycerine) with three fatty acids—oleic, palmitic and stearic. It is on the relative proportions of these fatty acids it contains that the solidity and melting point of a particular fat depend, e.g., the fluidity of human fat compared with the solidity of mutton fat at body temperatures. Oleic is the most fluid of the three fatty acids, palmitic and stearic being relatively hard. In general, fats are insoluble in water ; dissolve easily in ether and alcohol ; can be emulsified in water as fine dispersed droplets ; and are capable during digestion of being broken down into their constituent fatty acids, prior to rearrangement by the tissues.

The grease of the skin, the oil of the hair, and the wax of the ear are rather more complex fats known as *sterols* ; and even more complicated combinations of fats with phosphorus are found in nervous tissue and in the bounding membranes of cells generally, where they are responsible for some of the surface phenomena alluded to in the previous chapter.

2 The *carbohydrates* are in plants the immediate products of the synthesis of water and carbon dioxide, and serve in animals as an important source of energy. They are compounds of carbon, hydrogen and oxygen, and their essential saccharide unit CH_2O is used as a building brick in the body to form carbohydrate compounds of increasing complexity.

The *monosaccharides* include glucose, the sugar of fruits, also formed in the body by the digestion of cane sugar and starch; and fructose.

The *disaccharides* include cane sugar; the maltose of fermenting grain and barley; and the lactose of milk.

The *polysaccharides* are complex substances of high molecular weight. They include *starch*, found in all vegetable foods, potatoes, root crops and cereals, as grains within the plant cells, and ultimately converted by digestion into glucose. *Glycogen*, or animal starch, is very important; resembling starch, it is stored as granules in all the tissues but particularly in the liver and muscles. And it is the liver glycogen which is the great energy reserve of the body, mobilized when required by conversion into glucose which re-enters the blood-stream. There is also the rough *cellulose* of plants, digestible by herbivorous animals but not to any extent by man.

3 The *proteins* are the most important constituents of protoplasm and the body cannot long endure deprivation of them in the food; they occur in quantity in lean meat, cheese, and the vegetable pulses. They are extremely complex unions of carbon, hydrogen, oxygen and nitrogen, and usually of sulphur also; they are colloid substances, soluble in water and coagulating irreversibly on heating. The essential unit of the protein molecule is the *amino-acid*; and though there is an enormous variety of different animal and vegetable proteins, the only chemical difference lies in the particular

amino-acids contained in the protein molecule, their properties, and the way they are arranged. This is of some importance to man as a consumer, as the more essential amino-acids are only found in the " first-class proteins " such as those of meat.

The protein of each animal and vegetable species is quite different from all others ; on this specificity, and also on the reaction a foreign protein excites in the living tissues of man, depend the phenomena of *immunization* (e.g., against diphtheria) and *allergy* (e.g., nettle rash). Protein is, in fact, the basic chemical unit of protoplasm in all living cells, and different tissues possess their own characteristic proteins : the red haemoglobin of blood ; the slimy mucoproteins of mucous secretions ; the casein of milk ; egg albumen ; muscle protein ; and the complex nucleoproteins linked with phosphorus contained in cell-nuclei. We have already seen that proteins as a whole can function both as weak acids and as weak alkalis, and thus maintain a buffering neutrality to changes in the reaction of tissue fluids.

Enzymes. It is a striking fact that the complex changes of chemical breakdown and resynthesis are performed in the body much more rapidly and easily than in the laboratory ; indeed artificial synthesis is not yet possible in some cases. Thus starch is completely converted into maltose by the saliva within the space of a minute, though this would take several hours' boiling for the chemist to achieve.

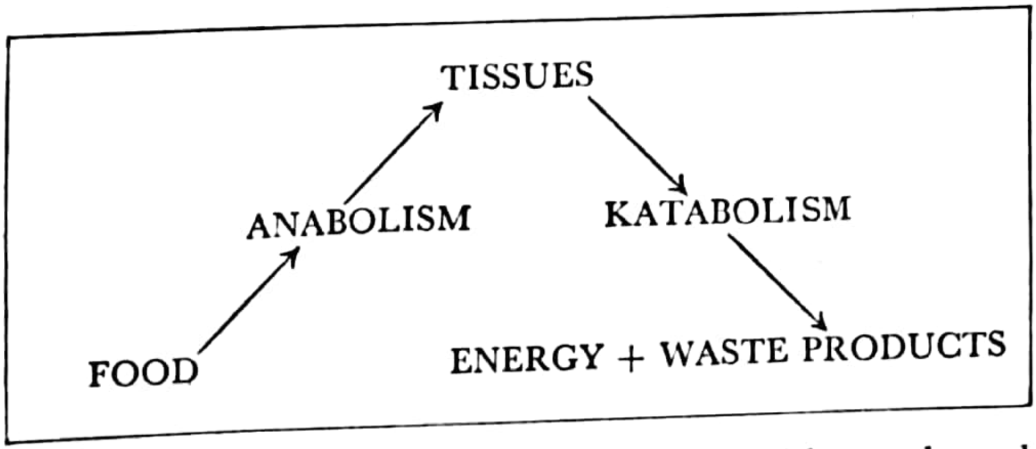
This facilitation of chemical changes in the body is due to what are known as *enzymes*. We are familiar in inorganic chemistry with substances called catalysts ; these need only be present in minute amount to accelerate enormously certain reactions in which they are not themselves consumed. Enzymes are the catalysts of the organic reactions of the body ; they are complex colloidal materials sensitive to changes in the environment and preferring a definite degree of acidity or alkalinity for their optimum performance, e.g., the pepsin of the acid gastric juice, the trypsin of alkaline pancreatic secretion. They facilitate breakdown, synthesis, and oxidation processes ; but especially a process known as *hydrolysis*, the addition of water to the molecule of the substance to be acted on, a common preliminary to its disintegration.

Enzymes are specific, each acting on a particular material only, known as its *substrate*, e.g., the amylase of saliva acts only on the starch of the food ; and all the digestive juices contain different enzymes designed to act on the various constituents of the food—lipases for fats, proteases for proteins, carbohydrases for the sugars and starches. These do not act at all on other substances or even on other members of the same group of food-substance. Most enzyme reactions are reversible, the enzyme being capable of pushing the chain of events either way. Enzyme reactions fall in two main groups : the processes of digestion occurring in the cavity of the bowel from the outpouring of digestive juices ; and the more intimate reactions, such as oxidation, occurring within the individual cells of the tissues.

Metabolism. Physiologically, the life of man can be regarded as a continual production of energy by oxidation (burning) of the food he consumes ; and the expenditure of this energy in (*a*) maintaining a constant body temperature above that of his surroundings, and (*b*) movement.

We have already pointed out that the balance sheet for this energy intake and output is an exact one ; food burnt within the body liberates the same energy as it does when oxidized experimentally in the laboratory. But, although the physical laws of thermodynamics are as applicable to the body as to the stoking of a furnace with coal, the human arrangements are complicated by the fact that the food is not burnt *as such*, but only after it has been digested and assimilated into the living tissues. It is as if the coal had to become a part of the furnace itself before being used up ; for only a few exceptional substances like alcohol can be burnt directly without first becoming part of the living protoplasm.

Thus there is a recurrent cycle of activities, known overall as *metabolism*. Part of this is the process of building-up or repair, of assimilation of food into the tissues—*anabolism* ; part is the breaking down of these tissues with the liberation of energy and the excretion of wastes—*katabolism*. Both are going on at the same time, all the time, though their relative proportions obviously vary under different circumstances. Anabolism preponderates in the active growth of children, katabolism during starvation when the body draws on its own reserves.



The waste products are excreted by the kidneys, bowel, lungs and skin, and consist mainly of water, carbon dioxide, and certain nitrogenous breakdown products of protein such as urea, which are mostly expelled in the urine, though to a lesser extent in the faeces.

During fasting, if the body is at complete rest, there is an essential minimum of energy output required to maintain its warmth and the movements of respiration and of the heart. This minimum can be measured, and is then known as the *basic metabolic rate* and, though of the same order of magnitude for everyone, varies from person to person in virtue of their different sizes. This is because most of the energy is expended in making up for heat loss from the surface of the body and is therefore directly proportional to the surface area. Basal metabolism is rather higher in men than in women, and higher still, in proportion to body weight, in young children. Each individual has his normal metabolic rate, predictable from height and weight, and this is much increased in fever, in excitement and anxiety, and also by the over-activity of the thyroid gland which has an intimate control over metabolism. In thyroid deficiency, as in cretinism, the metabolism is considerably below normal.

From the basal rate we can estimate the calorie value of the food required to maintain the essential activities of the body without allowing actual starvation ; this is in the region of 2000 calories per day. Below this level the body begins to fall back on its own reserves ; the fat and glycogen stores are first consumed, and then the less essential tissues such as the muscles and glands digest themselves to feed the brain and heart—with eventual death when the latter organ fails.

CHAPTER V

FOOD, DIGESTION, ABSORPTION

Foodstuffs. Each of the three great classes of foodstuff has a definite *heat value*, the number of calories liberated on burning 1 gramme of the material. These values are :

1 gramme of protein = 4·1 calories
1 gramme of fat = 9·3 calories
1 gramme of carbohydrate = 4·1 calories,

where the calorie is a standard unit of heat, the amount required to raise the temperature of a litre of water through one degree Centigrade. (In English measures, a gramme is about $\frac{1}{30}$ of an ounce, and 60 calories are required to heat a pint of water from freezing to boiling point.)

These foods not only supply energy but also replace wear and tear in the tissues, and here the proteins occupy a special position. Whereas any of the foodstuffs will be used for the production of energy, only proteins can be used for cell building. As far as energy production is concerned, fat is more economical than either of the others, for not only does it provide twice as much heat but it is commonly used in much purer form, as in butter or lard.

In practice, nitrogenous foods such as protein are not an economical way of obtaining energy ; in a normal mixed diet, the fats and carbohydrates are used to meet the ordinary energy requirements of the body and proteins serve only to repair tissue breakdown. Man cannot obtain his necessary energy from protein alone; he would have to eat some 5 lb. of lean meat daily to obtain his basic minimum of 2000 calories, and 7½ lb. for his normal 3000 odd calories, an amount impossible for most people to digest. A diet of lean meat and green vegetables is certainly a cure for obesity, but only by producing a modified form of starvation. Nor is protein stored as such to any extent in the body, except during growth when some is laid down in the muscles. So we see that protein is not only an essential of the diet, it must also be a regular daily constituent; but it has no advantages as a source of energy over fats and carbohydrates, which are capable of considerable variation and mutual interchangeability.

Respiratory Quotient. We can obtain a clue to the particular substance which is being oxidized in the body to provide energy by comparing the oxygen used up in the process (and contained in the inspired air) with the carbon dioxide evolved (and got rid of in the expired air). Thus the burning of carbohydrates may be represented by the simple chemical equation:

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O,$$

and here the respiratory quotient $\frac{CO_2 \text{ expired}}{O_2 \text{ inspired}}$ would be exactly 1. Since different materials are being burnt at the same time, the actual respiratory quotient estimated by analysis of the inspired and expired air depends on the relative proportions of the foodstuffs, whose respective quotients are:

carbohydrates = 1·0
protein = 0·8
fat = 0·7

Thus the actual quotient is always less than 1, since a purely carbohydrate diet is never met with in practice;

the quotient represents the gross result of oxidation of the average mixture of foodstuffs consumed in the body.

From the energy point of view any of the foodstuffs may be utilized, and carbohydrates and proteins are spoken of as *isodynamic*, because an equivalent weight of each gives rise to the same amount of heat. Carbohydrates and fats in the proportion of rather more than 2 : 1 also provide the same number of calories ; and so they can replace each other in the diet in these proportions without altering the available energy. We have seen that, though protein is theoretically interchangeable in the same way, an upper limit to its use is set by the capacity for its digestion and assimilation. Since protein is not stored in the adult body, any taken in the food is rapidly broken down and excreted as nitrogenous compounds in the urine and faeces, i.e., there is a normal state of nitrogenous equilibrium and with an already adequate mixed diet any increase in the amount of, say, meat protein, simply results in a corresponding increase of nitrogenous wastes. This is quite different from the situation with fats and carbohydrates, for an excess of either of these is stored in the body as *fat*.

Protein is broken down by digestion into its constituent amino-acids ; these enter the blood-stream, where they partake in continuous equilibrium and interchange with the protein of the body cells, the latter taking up such amino-acids as they require for repair. Residual amino-acids are disintegrated ; their nitrogenous part is lost as urea through the kidneys, the rest is burnt down to carbon dioxide and water. We have already seen that all food proteins are not of the same biological value, for only some contain those essential amino-acids which cannot be synthesized in the body ; these are the *first-class proteins* of meat, wheat, etc.

The other *second-class proteins* lack some of the essential amino-acids or are made up largely of inessential ones ; gelatin is an example of this class. A deficiency of the essential acids results in a loss of appetite and failure of growth ; to make this vital provision, animal protein is more economical than vegetable, though the latter may be adequate if the diet is sufficiently varied.

Inorganic Foods. *Water* constitutes some 70 per cent of the body weight ; most of it is within the living cells, but it also provides the bulk of the intercellular fluid and the blood. There is a rapid interchange-equilibrium between the water in all these sites, with the result that the tissue water content is maintained fairly constant. The osmotic pressure of cell fluids, the blood, and the secretions of the various glands is also maintained at much the same level ; and the regulating action of kidney excretion is such that the blood is not diluted or concentrated to any extent by even gross changes in the quantity of water drunk or contained in the food. But the latter is not the only source of water, for it is also formed by the oxidation of foodstuffs. And it is got rid of via the skin as obvious sweat or invisible evaporation, and in the exhaled air from the lungs, as well as in the urine and faeces. The average daily *water balance* for an adult is roughly as follows :

Intake		*Output*	
Drunk as such	= 2½ pints	Lost in urine	= 2½ pints
Contained in food	= 1⅓ pints	From skin surface	= 1 pint
From oxidation of food	= ½ pint	From lungs	= ⅔ pint
		In faeces	= ⅙ pint
Total	= 4⅓ pints	Total	= 4⅓ pints

The particular way in which water is lost varies with circumstances and when one route predominates the others are used less, e.g., the excessive sweating of hot weather reduces the amount of urine excreted. But there is a daily minimum urinary output of some ½–1 pint, which is necessary to carry out in solution the nitrogenous wastes.

The " insensible " loss of water by evaporation from the skin and in the exhaled air is very considerable and amounts to some 1½–2 pints every 24 hours. A continued loss of water from a relative excess of output over intake produces *dehydration*, and the loss of more than a fifth of the body water in this way is usually fatal. An excessive intake also has its dangers and can produce fatal *water poisoning* by so lowering the osmotic pressure of the tissue fluids that the cells swell up and burst.

The *mineral salts* are equally essential to life, though in small amounts. Complete deprivation results in loss of appetite, illness and death, even if the diet be otherwise normal. *Sodium* is mainly taken as its chloride, in common salt and in the food. *Iron* is abundant in meat, vegetables and offal, but not in milk ; it is essential for the formation of haemoglobin, and any deficiency, such as is common in pregnancy, leads to anaemia. *Calcium* occurs in greatest concentration in milk and cheese, and to a lesser extent in eggs and vegetables ; there is little calcium in meat or bread. The calcium requirement is greatest in growing children and pregnant women, for it is essential to the proper development of bones and teeth. It is also indispensable to the clotting of the blood, and has a good deal to do with the sensitivity of the cells of the nervous system to stimulation.

The other mineral constituents of the food have been touched on in the previous chapter.

The Vitamins. If an animal is fed on a diet which contains adequate amounts of fat, carbohydrate and protein and salts, *but in which these constituents have been purified*, it becomes ill, stunted, and eventually dies. Yet these changes may be entirely prevented by the daily addition of a teaspoonful of milk to this artificial diet. This is because natural foods contain minute quantities of organic substances known as vitamins, or accessory food factors. These are essential for the proper utilization of the food ; to allow normal growth and development in the child, and to maintain health in the adult. Yet in themselves they contribute nothing to the energy requirements or tissue repair of the body.

The more important vitamins we are concerned with are the following :

Fat-soluble vitamins :

A. Growth ; anti-infective.
D. Bones, teeth ; anti-rickets.
E. Fertility.
K. Clotting of blood.

Water-soluble vitamins :

B_1. Nervous function ; anti-neuritic.
B_2. Oxidation processes of cells.
C. Anti-scurvy.

Vitamin A is essential to growth. Its absence causes stunting, susceptibility to infective disease, a horny overgrowth of the skin which leads to blindness by spreading to the transparent cornea of the eye, and eventual death. It has also some relation to night-blindness and to disorders of the central nervous system. Like all the fat-soluble vitamins it is held in the fats of the food, in milk, butter, and particularly in fish-liver oils ; and it is stored in the human liver. It is interesting to note that it is always originally formed by green plants, either in the grass used for grazing or in the minute diatoms of the sea.

Vitamin D is also contained in cod-liver oil, butter and cream, and its main function is the regulation of the absorption of calcium and phosphorus from the bowel and their interrelation and utilization in the body. It therefore exerts a major influence on the proper growth and hardening of bones and teeth and any deficiency in childhood leads to rickets and dental caries. But this same calcifying property becomes dangerous if the vitamin is given in excess, when hard deposits may be formed in the heart and kidneys ; to produce these effects, however, the excess has to be many thousand times the normal dose.

Vitamin D is also formed in the skin by the influence of the ultra-violet rays of sunlight on a particular fatty constituent of the skin. It is for this reason that heavily-pigmented children from Latin and tropical countries sometimes develop rickets when moved to a temperate zone where the sun's rays are much less direct.

Vitamin E is essential to normal fertility ; no obvious sign may exist of any deficiency but the young embryos of animals deprived of it fail to develop and die within the womb. It is found in high concentration in the germ of wheat.

Vitamin B is a complex of factors, which have only recently been separated. Its original discovery was due to the observation that a diet of rice, polished so as to remove the husks, causes *beri-beri* ; this is a disease of the nervous system and heart, with weakness, paralysis, swelling of the limbs and heart-failure. The vitamin is contained in the husks of rice, and is abundant in yeast, milk, meat and wheat-germ.

B_1 is the main anti-beri-beri or anti-neuritic factor.

B_2 is more concerned with the vital cellular processes of oxidation.

A third factor is *nicotinic acid*, which prevents the disease of *pellagra*, a scaling of the skin with associated mental changes found in some parts of Africa and in the Deep South of the United States.

Vitamin C acts against scurvy. This has long been recognized as a disease due to deprivation of fresh fruit and vegetables; its main features are haemorrhages, anaemia and indolent healing of wounds and fractures. Captain Cook knew something of its cause and cured his sailors with limes and lemons; and we now know that it is a specific compound—*ascorbic acid*—found in oranges, lemons, other fruits and green vegetables.

The majority of the vitamins are of known chemical composition and can be synthesized artificially, or otherwise obtained, in pure crystalline or oily form. The only evidence we have of their effects is what happens when the body is deprived of them; then, just as the smooth running of a machine is interrupted for lack of lubricating oil, certain deficiency diseases make their appearance. We have emphasized that, though the vitamins are therefore essential to health and the normal utilization of food, they are not themselves foodstuffs and do not compensate for an inadequate diet. Further, in the ordinary adult living on a good mixed diet there is little or no need for the addition of vitamin preparations. This is not the case with the relatively greater needs of growing children, particularly if living on a restricted diet in wartime; for them special supplementary provision of cod-liver oil and orange juice has been made in time of war.

Digestion and Absorption

The Digestive System. Food passing through the mouth enters an expanded cavity behind, the *pharynx*, which is also common to the air-passage at this level. It then travels down the gullet (*oesophagus*) to the *stomach*, thence to the coils of *small intestine*, and then into the large intestine or *colon*. The waste matter in the food finally reaches the lowest part of the large bowel, or

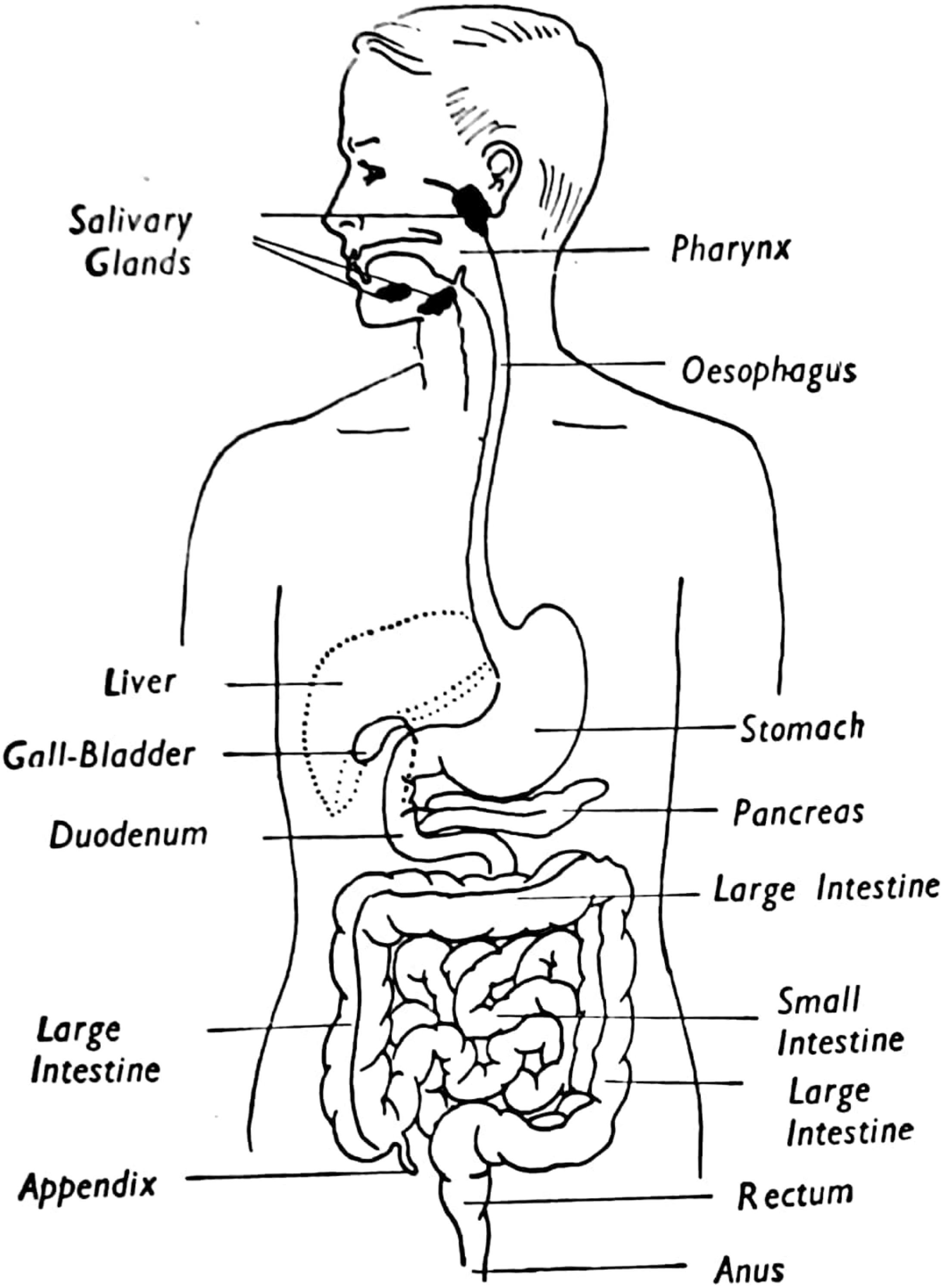


FIG. 8.—The Digestive System.

rectum, and is expelled through the short *anal canal*. At various points along the digestive tract certain glands are situated and discharge their secretions into it. These are: the three pairs of *salivary glands* around the mouth;

the *pancreas*, below the stomach ; and the *liver*, which overlies the stomach.

The Diet. The average daily energy requirement of a working man is 3000 calories. An adult woman needs 2500 calories, simply in virtue of her smaller size and surface ; and sedentary workers need correspondingly less. In fact, because of an inevitable loss of calories in preparing and cooking food and in digestion, an extra allowance is necessary, and the calorific value of the food for an adult man, *as purchased*, is some 3500. To maintain health, a diet should possess this calorie value ; it must also contain protein, fat and carbohydrate in the proportions indicated below ; it must include enough fresh food to supply the necessary vitamins ; it should have enough mineral content ; and finally *it must be palatable*.

Protein should supply one-sixth of the calorie needs, i.e., there should be at least 100 grammes a day, at least half in the form of first-class protein of animal origin. If this minimum is provided, an excess serves no particular purpose. It is conventional to assume that extra meat is necessary for heavy workers, but this is not in fact the case. What protein does do, more than other foods, is to give a fillip to metabolism generally, a sort of cocktail which increases the rate of heat-production and helps to keep one warm in cold weather.

Carbohydrates form the largest part of most diets, for they are cheap and easily obtainable, in the form of bread and other filler foods such as potatoes. The optimum daily need is some 500 grammes. Though it is unlikely that anyone would eat less than the minimum amount, there *is* an absolute minimum ; below this absolute minimum the carbohydrate : fat ratio is disturbed so that fats are not completely burnt in the body and acid products accumulate in the tissues.

Fat is valuable because of its high energy value. A normal diet contains only one-seventh of its weight of fat (some 100 grammes), but this supplies a quarter of the total calories; and this concentration of bulk is exaggerated still more by the small amount of water it contains compared with other foods. Though interchangeable to a considerable extent with carbohydrate as an energy source, fat has certain desirable qualities of its own. For instance, its very slow absorption after meals prevents the recurrent hunger which would otherwise be felt with a largely carbohydrate diet; and for really heavy work in cold or Arctic conditions, a large amount of fat is the only practical way of supplying calorie needs which may rise as high as 8000 a day.

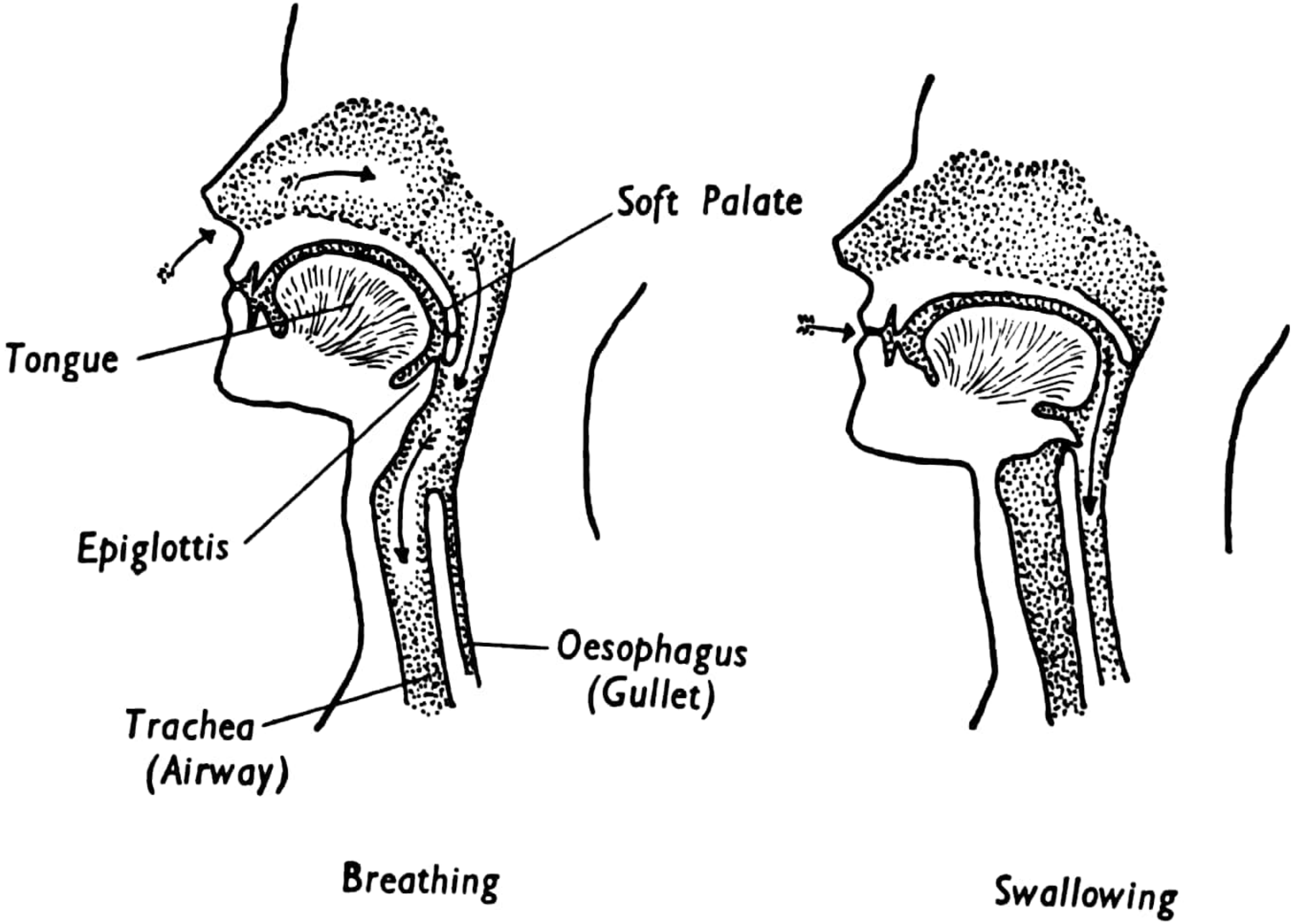
The Object of Digestion. Digestion secures the conversion of the complex and insoluble constituents of the food into simpler substances which dissolve and diffuse through the lining of the intestine to enter the blood or lymph, and with which the tissues can deal. Thus all carbohydrates must be reduced to the simplest monosaccharide form, such as glucose, or the cells will be unable to assimilate them. The fats must be hydrolysed to fatty acids and glycerol—though some fat enters the lymph unhydrolysed as finely-emulsified globules; and the proteins are split up into their constituent amino-acids. In dealing with the latter, the body displays considerable versatility and ingenuity; to convert the protein of cheese into one of the human forms of protein is equivalent to taking a Meccano model to pieces and picking out the right bits to build up a new model of one's own liking.

Digestion is accomplished by the enzymes contained in the digestive juices, formed in the various glands stationed along the length of the digestive system; each specific foodstuff needs a corresponding enzyme to break it down.

The Mouth. Entry of food into the mouth provokes a flow of saliva. This is a reflex or automatic action ; the stimulation of the taste nerve-endings is transmitted to the brain and relayed back along the nerves controlling salivary secretion. But there may also be what is called a " psychic " secretion, at the mere anticipation of food ; and this is an example of a conditioned reflex in which an association of ideas has the same effect as the original physical stimulus itself.

The saliva is a mixture of the secretions of the three salivary glands on either side : the *parotid* in the cheek (in front of ear) the *submaxillary* beneath the lower jaw, and the *sublingual* under the tongue in the floor of the mouth. It contains *mucin* to make the food a slippery easily-swallowed mass ; *calcium phosphate*, which is deposited on the back of the teeth as tartar ; and an enzyme, *ptyalin*, which digests starch to sugar (maltose). It is a curious fact that much of salivary digestion actually occurs in the stomach. Food does not remain long in the mouth, but the swallowed mass still contains ptyalin which continues to exert its digestive effect in the stomach, until complete penetration of the food by the acid gastric juice brings the process to a stop after half an hour. There is a normal continuous slight secretion of saliva between meals, which is stopped by fear and by certain drugs such as atropine, which dry up the mouth.

Swallowing. The object of chewing is the production of a round mass, or *bolus*, of food which is passed down to the stomach in the act of swallowing. Now, although in the lower part of the neck and in the chest the air- and food-passages are quite separate, in the upper part of the neck there is a common cavity for food and air extending up as far as the base of the skull. This is the *pharynx*, situated immediately in front of the vertical column. In swallowing, it is essential to prevent



Breathing

Swallowing

FIG. 9.—The mechanism of swallowing. Note how the palate moves upward to block the back of the nose, and the epiglottis down to shut off the windpipe.

food passing upwards into the nose round the free edge of the soft palate, or downwards into the airway to the lungs. Therefore, in swallowing the soft palate is apposed to the back wall of the pharynx so as to seal off the nasal cavities ; and the *epiglottis*, an elastic flap situated behind the root of the tongue, bends over backwards to close the entry into the larynx. At the same time the larynx as a whole is pulled bodily upwards and then recedes again (Fig. 9).

The Stomach. The stomach is a hollow muscular organ lined by a glandular *mucous membrane* which secretes the gastric juice. It has an opening at either end, to connect it with the lower end of the gullet and the beginning of the small intestine, the duodenum ; and these openings are normally kept closed by tight rings of muscle, or *sphincters*. Small amounts of gastric juice are present in the resting state ; the mere sight of food or its entry into the mouth excites a reflex secretion ; and more is formed when the food actually arrives in the stomach. As much as a pint of gastric juice may be secreted after a heavy meal, the process continuing for 2–3 hours.

The secretion is strongly acid, owing to the presence of up to $\frac{1}{2}$ per cent hydrochloric acid ; but some of this is neutralized by combination with mucus, so that only some 0·3 per cent is free. There is a good deal of mucin ; and the special enzyme of gastric juice is *pepsin*, which is concerned with the digestion of protein. A few normal individuals are completely devoid of acid in their secretion ; though in itself of little importance, this may be associated with an absence of certain other essential substances—the cause of pernicious anaemia. The gastric juice acts on the food in two ways : in virtue of its acidity, and by its enzyme action. The acid alone is responsible for minor breakdown of certain foods, e.g., the more complex sugars ; but most of the work is done by the pepsin, which completes the first stage of protein digestion, converting them to *peptones*. It also sets free the fat of the food in liquid form by dissolving the fibrous framework around its globules, thus preparing it for digestion in the duodenum.

There is also another enzyme, *rennin*, which turns milk into a casein clot, which is then digested by pepsin in the ordinary way.

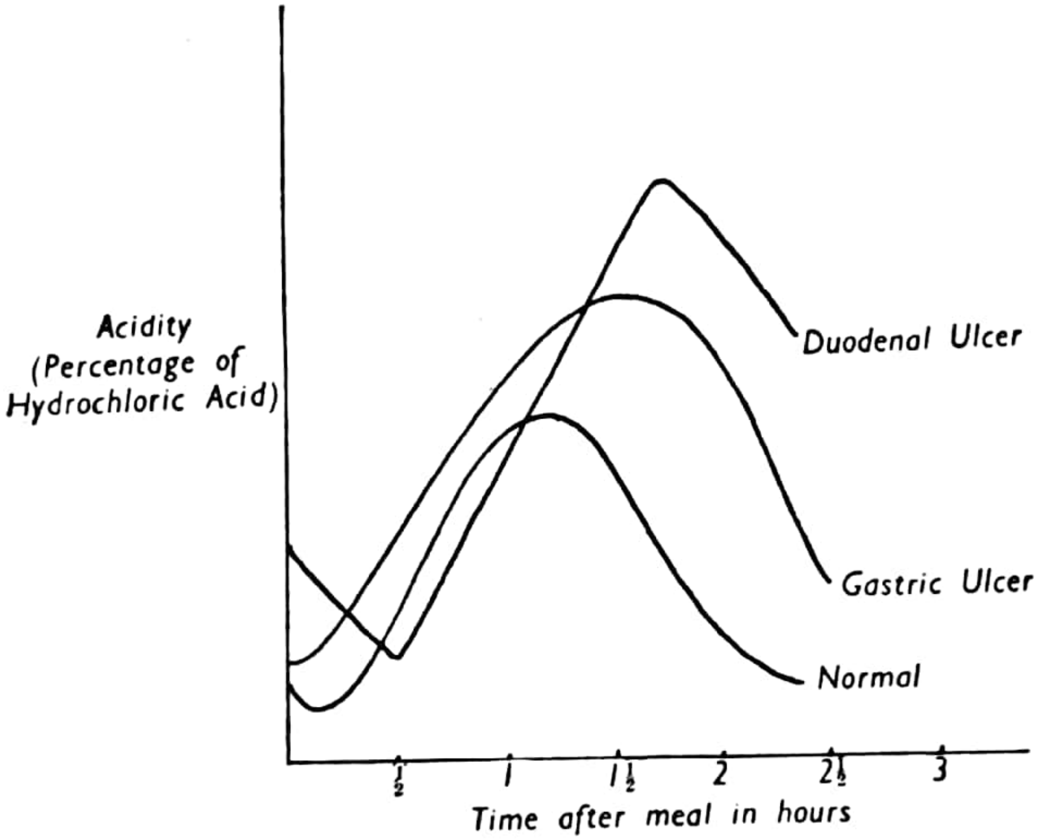


FIG. 10.—Gastric secretion of acid after a meal in normal individuals and in ulcer cases.

The response of gastric secretion to food may be studied by the experimental administration of a standard meal of gruel, and then withdrawing the stomach contents at intervals for analysis. The findings may then be plotted as a curve. Fig. 10 shows the results of such an experiment, with the usual rise and fall of hydrochloric acid levels. It also shows the findings in certain diseases, for such " test meals " also give us a clue to the nature of stomach derangements. Thus in gastric ulcer the acid secretion reaches an unduly high level ; and in duodenal ulcer the resting juice in the organ, before any food has been taken, contains a considerable amount of acid, which aggravates the ulcer by its action on the mucous membrane. In the latter case, the first effect of a meal is to lower the acidity ; hence the need for frequent small feeds in duodenal ulceration to prevent the ill-effects of over-acidity on the unprotected stomach lining.

The food is being constantly propelled from the left side of the stomach towards the right-hand duodenal exit, by means of regular waves of contraction in its muscular wall. For the first ½–1 hour after a meal, the duodenal opening remains closed by local muscular spasm ; then it opens at intervals and allows stomach contents to pass in intermittent spurts into the duodenum. By the end of gastric digestion, in 3–4 hours, all the food has passed through ; the opening then relaxes, and some duodenal contents and bile regurgitate back into the stomach. Fluids leave the stomach long before solid food, and taken alone they enter the duodenum in a few minutes ; and, as we have noted, fats remain in the organ much longer than carbohydrates.

Although the standard anatomical position of the stomach is given as the upper part of the abdominal cavity, rather to the left, it is important to realize that in fact the organ undergoes considerable changes in position. These are due not only to changes in the position of the body as a whole, but also to emotional influences ; we speak of " our heart being in our boots ", and what actually happens is that the stomach does drop considerably, perhaps even as low as the pelvis. The general motility of its muscular wall, and its rate of secretion, are so intimately affected by emotional states that it is not surprising that many cases of dyspepsia or actual ulceration are of nervous origin.

Small Intestine. Here we have to consider the action of three different digestive juices :

(i) the *pancreatic juice* ;
(ii) the *bile*, formed by the liver ;
(iii) the *intestinal juice*, the secretion of the small glands of the bowel lining.

The bile and pancreatic juice are discharged simultaneously into the duodenum by means of ducts from the pancreas and liver which open in common ; the intestinal juice is formed along the whole length of the small bowel.

The *pancreatic juice* is formed in two ways. There is a response to the taking of food which is a nervous reflex ; but there is also a much more important response to the entry of acid gastric contents into the small intestine. This latter mechanism is a beautiful example of the work of chemical messengers or *hormones* in the body. When stomach contents enter the intestine, some of the acid passes through the bowel wall and, as it does so, extracts from it a potent stimulating agent, called *secretin*, which enters the blood-stream and is carried to the pancreas. Here it acts as a specific stimulus to the secretion of the pancreatic juice. The alkaline pancreatic juice then enters the duodenum and neutralizes the acid influx, thus automatically bringing to a stop the mechanism for evoking pancreatic secretion. The next spurt of gastric contents starts a fresh cycle, and so on. Thus, by this chemical arrangement, pancreatic secretion is exactly suited to the needs of digestion. The pancreatic juice is about as alkaline as gastric secretion is acid, and it contains three powerful enzymes ;

trypsin, which completes the digestion of proteins to their constituent amino-acids ; *amylase*, which hydrolyses starch and other carbohydrates to glucose ; and *lipase*, which breaks up fats into fatty acids and glycerol. It is interesting to note that the pancreatic juice will not function properly without the presence of the other two secretions. Thus protein digestion by trypsin does not occur unless activated by a special substance in the intestinal juice ; and fat digestion is enormously helped by the bile, which emulsifies the globules and so exposes a far greater area to the action of the lipase. The freed fatty acids will form soaps if the intestinal contents become sufficiently alkaline.

The *bile* is secreted by the liver. It is not only a digestive juice but also a means of getting rid of the breakdown products of the haemoglobin in the red cells of the blood. Since the bile is therefore being formed continuously, though it is only needed in the bowel during digestion, it has to be stored in the intervals in a small bag on the undersurface of the liver, the gall-bladder. From this reservoir the bile duct travels down to join the pancreatic duct, and opens with it into the duodenum. The muscular gall bladder is full before meals, and particularly distended in starvation ; the entry of food into the duodenum relaxes the spasm of the muscle guarding the opening of the duct, and the bladder contracts to discharge bile into the bowel. Certain swallowed substances are particularly efficient in exciting this response, e.g., Epsom salts and fats.

The composition of the bile. The bile is being continuously secreted by the liver cells to a total of some 1½ pints a day, and the rate of production is accelerated by meals of fatty or protein content. It is interesting to note that one of the most potent stimulants to its production is the presence of bile itself in the duodenum.

It is a slightly alkaline, viscid green fluid. The colour is due to the *bile pigments*, breakdown products of the

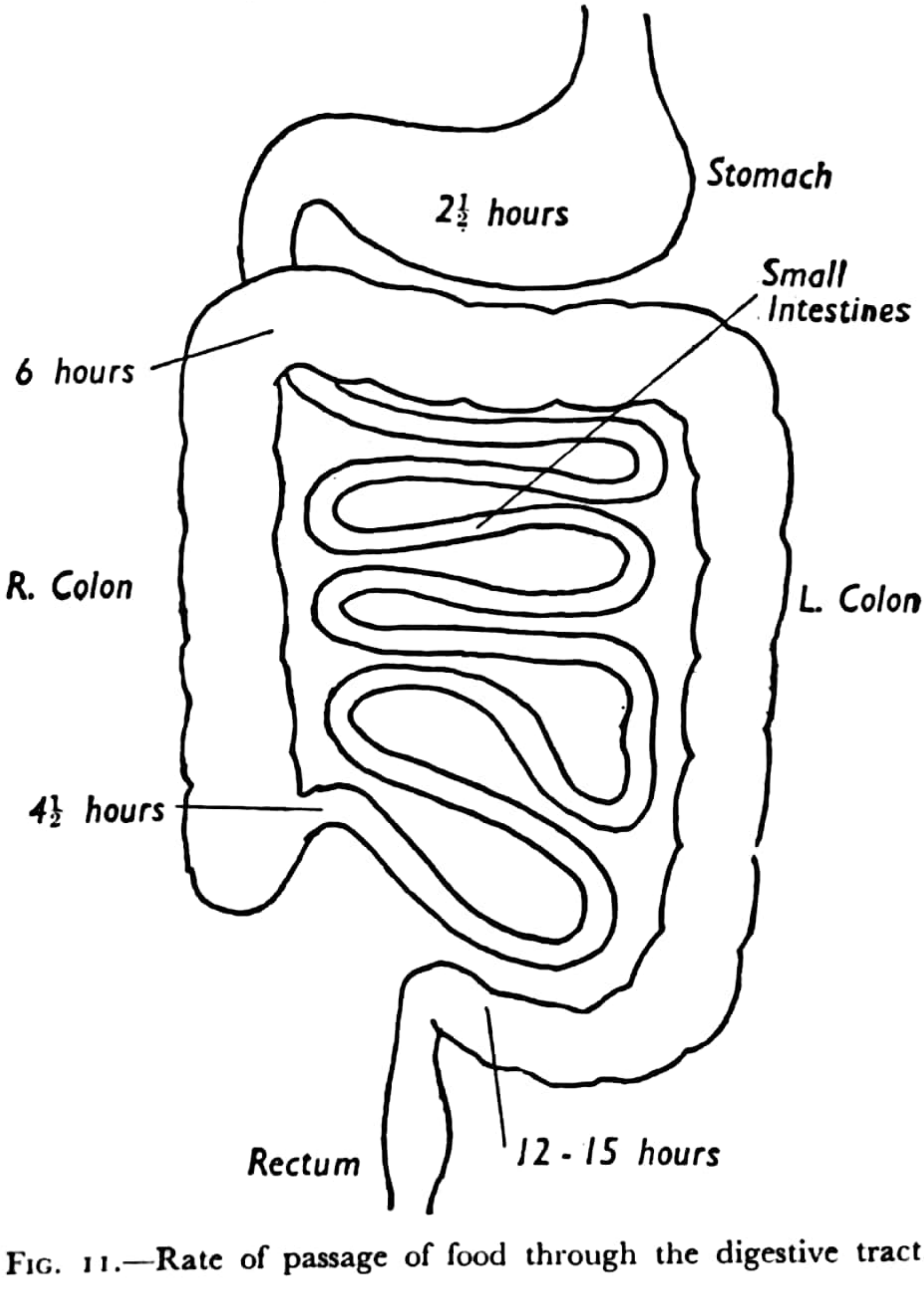


FIG. 11.—Rate of passage of food through the digestive tract.

haemoglobin from worn-out red blood cells, which are disintegrated in the liver and spleen. It is these, still further altered and mixed with undigested food, which give the faeces their characteristic brown colour. And in *jaundice*, due to some blockage of the bile duct which prevents the pigments entering the bowel, the faeces remain pale and clay-coloured ; while the dammed-up bile overflows into the circulation and stains the skin its typical yellow colour. The *bile salts* are the sodium compounds of certain complex acids and are of the greatest importance in fat digestion. For, though the bile contains no enzymes of its own, its salts finely emulsify the fat of the food to facilitate its digestion by the lipase of the pancreatic juice. The fats, now split into glycerol and fatty acids (or soaps), together with the bile salts, then traverse the bowel wall ; here, in the individual cell, globules of neutral fat are reformed and absorbed, and the bile salts are returned by the blood stream to the liver to be used over and over again.

The *intestinal juice* is secreted by numerous tiny glands in the wall of the small bowel throughout its length. It contains a number of enzymes, which act not so much on the food itself as on the breakdown products of the digestion already carried out in the stomach and duodenum above. And we have already seen that it contains an activator for the proper functioning of the pancreatic trypsin. It also contributes a large amount of water to facilitate the solution and absorption of digested food. On the whole, secretion and digestion predominate in the upper coils of the small bowel, and absorption of the digested products into the general circulation in the lower part ; but both processes are everywhere going on simultaneously to some extent.

The **Large Intestine** is little concerned with digestion or absorption of food, for most of this has been accomplished by the time the food reaches the lower end of the small bowel. This is certainly true with an ordinary mixed diet containing plenty of meat. On a mainly vegetarian regime, however, a considerable part of the food reaches the large intestine, where a little is absorbed, but most simply goes to swell the bulk of the faeces. However, there is one absorptive function of importance, the taking-up of water from the faeces. These enter the large bowel in a fluid state ; there they lose four-fifths of their water content, becoming quite solid by the time the lower (left) half of the colon is reached. The further passage of the hard faeces is lubricated by the scanty mucous secretion of the glands in the wall of the bowel. A considerable part of the excreta is composed of the enormous numbers of bacteria found in the large bowel ; the large bowel is here in contrast with the stomach and upper small intestine which are relatively sterile. As a result, an abdominal wound which penetrates the large intestine may be very dangerous, since it liberates bacteria into the peritoneal cavity, setting up a virulent peritonitis.

The movements of the intestine. The general principle of movement everywhere in the bowel—stomach, small and large intestine—by which it propels onward its contained food, is that of *peristalsis*. This is a rhythmically recurring wave of contraction which travels down a segment or loop of bowel, presenting a localized ring-like spasm at any particular point and is succeeded by a wave of relaxation. Peristalsis is not dependent on any central control and continues in an experimentally isolated coil of bowel, for it is brought about by the regulating action of a nerve plexus lying between the muscular layers of the intestinal wall itself ; this plexus forms a continuous network along the whole length of the bowel. It is, however, subject to considerable modification by influences from the central nervous system, particularly those of an emotional nature ; these affect both the rate of successive waves, and their amplitude. In the small bowel, certain other movements occur to mix the food thoroughly, e.g., *segmentation,* in which a length of intestine is shut off into a number of sausage-shaped segments by areas of ring spasm ; these segments change and reform from time to time.

Regular easy peristalsis does not occur in the colon, for here the problem is one of storage of the faeces until the taking of a fresh meal makes it necessary to move on the contents of the lower end of the intestine. The entry of food into the stomach excites what is known as the *gastro-colic reflex,* a mass contraction of the large bowel which transfers the faeces rapidly from right to left colon, and from left colon to rectum. The process of expulsion of the faeces outside the body is known as *defaecation,* and the rectum should normally remain empty until just before the act. Faeces enter the rectum by mass contraction of the large bowel after a meal, and this distension is felt as an urge to defaecate. However, the urge passes off if the call is not obeyed and the rectum relaxes again ; as a result, in the chronically constipated, the rectum always contains faeces and loses its power of regularly responding to distension.

The external opening of the anus is normally kept closed by the contraction of two guarding circular muscles or sphincters. In the act of defaecation these relax, the muscle coat of the rectum contracts, and the expulsion of the faeces is aided by the contraction of the abdominal muscles, which produce a rise in the intra-abdominal pressure.

It is a simple matter to determine how long it takes for the food to arrive at different stages of the bowel ; the method is to give a " meal " containing barium sulphate, which is opaque to X-rays, and which in consequence can be watched during its passage down the whole digestive canal (Fig. 11). The bulk of the stomach contents have passed on in 3 hours, though a small residue may persist up to 5 or 6 hours. The food arrives at the lower end of the small bowel and enters the large intestine after 4–4½ hours ; fills the right half of the colon in 6 hours ; and occupies the left half, ready for expulsion into the rectum, after 12–18 hours. These are average times and vary considerably ; part of the food may be delayed in the large bowel for several days.

The *faeces* themselves are derived in large part from substances formed in the intestine. They contain 70 per cent of water ; 15 per cent of mineral salts, such as calcium phosphate and iron ; and a considerable quantity of nitrogenous material, composed mainly of dead bacteria. This composition is considerably altered by increasing the cellulose (vegetable fibre) content of the food ; this increases the bulk of the faeces, stimulates peristalsis, and hurries their passage along the bowel, thus offering less opportunity for the extraction of water.

CHAPTER VI

UTILIZATION AND STORAGE OF DIGESTED FOOD

DIGESTION has achieved the transformation of complex insoluble food substances of high molecular weight into simpler soluble particles. These are capable of entering the circulation, and their transference from the bowel to the blood or lymph vessels is known as *absorption*.

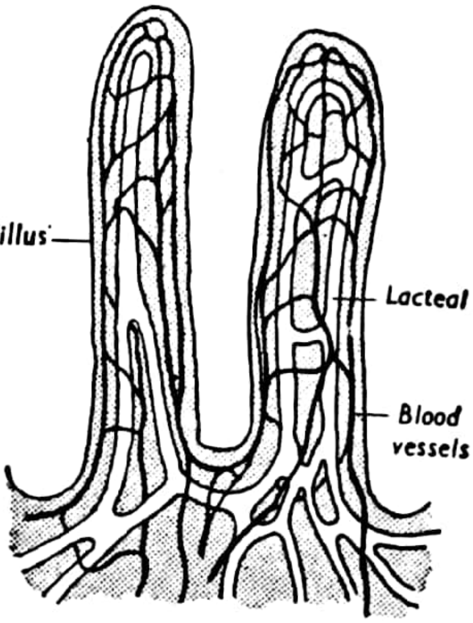


FIG. 12.—Villi of the small intestine with their lacteals and blood vessels.

After absorption, the liver plays a part of the first importance in the further utilization of the food; the anatomical arrangements of the circulation are such that a special *portal system* of blood vessels carries the products of digestion straight from the intestine to the liver; here they are dealt with in various ways before entering the general circulation.

Another anatomical point must first be emphasized. The lining of the small intestine is not a smooth surface, but a velvety pile made up of innumerable tiny hair-like processes, or *villi.* These project inwards and enormously increase the surface-area, available for absorption of the bowel contents into the blood-stream. Each villus is richly supplied with blood capillaries ; and each is also traversed by a central lymphatic channel, or *lacteal*, for carrying digested fat globules to a lymphatic plexus in the bowel wall, and thence to the main lymphatic trunks of the body. In the fasting state the villi are at rest ; but during absorption there is a constant pumping motion as they become alternately fully elongated or contracted and club-like. With this, there is a rhythmic squeezing out of absorbed materials into the general circulation (Fig. 12).

Water. All the water drunk is absorbed from the bowel, apart from a certain minimum retained in the faeces. Not much water absorption occurs in the stomach ; most of it takes place in the small intestine, and the remainder in the large bowel, where the fluid faeces are dried up and made more solid. The transference of water and dissolved substances across the bowel wall into the vessels of the villi is a complex procedure, and one not fully explicable in terms of the physical laws of osmosis, as it is greatly influenced by the selective activity of the living intestinal cells themselves.

Fats. Very little fat normally escapes digestion, and it is absorbed only in the small bowel. In digestion, it is first of all finely emulsified and then broken down into glycerol and fatty acids ; these may combine with common salt to form soaps. These products enter the intestinal wall, helped in their passage by the influence of the bile salts ; they then reform within the cells of the villi into globules of neutral fat which are transferred to the lacteal vessels and thence to the lymphatics of the intestine. After a fatty meal these channels, and the main thoracic lymph duct, are distended by a milky fluid, the *chyle*, opalescent by reason of the tiny fat particles or *chylomicrons*. The thoracic duct empties the fat into the blood-stream, where it joins up with the great veins of the neck, so that the blood serum may contain obvious fat a couple of hours after a meal.

This is the fate of reconstituted neutral fat. In addition, a certain amount of split fat—glycerol and fatty acids—finds its way directly into the blood-stream via the blood capillaries of the villi. But the major part of fat-absorption is by the lacteals and thoracic duct ; and division or injury of the thoracic duct cuts off the flow of fat into the blood-stream and produces starvation, emaciation, or eventual death.

Carbohydrates, having been broken down into their constituent monosaccharides by digestion, are entirely absorbed into the blood-stream from the small bowel. Only the simple forms, like glucose, can be so absorbed ; even cane sugar must first be hydrolysed before it is of any use to the body.

Proteins. The constituent amino-acids, set free by digestion, are absorbed into the blood and circulate throughout the body. Some are taken up by the individual tissues until an equilibrium is reached, and are used by them to replace disintegrative loss by wear and tear. The greater part of the amino-acids, however, is taken up by the liver and there undergoes an important process known as *de-amination*. As a result of this, the nitrogenous part is converted to urea and carried by the blood to the kidneys, for excretion in the urine, and the non-nitrogenous part is burnt in the tissues as a source of energy. It has been said that the amino-acids are the protein currency of the body, just as glucose is the carbohydrate currency ; small, universally-recognized coins, freely interchangeable, and capable of being built up at different depôts into the larger, more complex and individual proteins of special tissues. It would appear therefore that it might be possible to live on a diet containing, not the natural proteins of milk and meat, but their constituent amino-acids formed by preliminary artificial digestion in the laboratory. And this is, in fact, the case ; digests of casein and other proteins have been found of value in feeding patients after operations, and for the starved inhabitants of concentration camps, whose digestive systems could not cope with the complex original materials.

The Fate of the Foodstuffs in the Body. It is not altogether an easy task to follow the sometimes obscure paths of the individual food substances once they have been absorbed from the bowel. But some help has been made available by recent developments in atomic physics, with which readers may be familiar from another point of view. Physicists are especially interested in *isotopes* ; these are variants of the normal chemical elements, identical in their chemical behaviour, but having a slightly different atomic weight. Some of these occur naturally, e.g., " heavy " oxygen or hydrogen ; some are radio-active and manufactured artificially. Their practical importance in physiological research is that they can be used as " tracers " to label any particular compound in its passage and transformations within the body, for the isotope can always be picked out by the spectroscope or other means. Thus we can watch the fate of amino-acids by labelling them with heavy nitrogen, finding later that this has become distributed in the tissue proteins ; or we may follow the utilization of calcium in bone-building by feeding calcium phosphate in which the calcium is artificially radio-active, and noting the particular parts of the bone where the radio-active deposit is greatest.

Proteins. The ultimate fate of the constituent amino-acids of protein is partly to enter into the composition of the actual living protoplasm, partly to serve as a source of energy. In the latter function it is obviously on a par with the fats and carbohydrates ; in the former, it is irreplaceable.

We have seen that each protein of the food has to be taken to pieces in digestion and then reassembled in a particular way by each tissue which receives these pieces from the blood-stream. This reassembly produces a protein specific to each of the body tissues, i.e., muscle protein is chemically different from liver protein, and both are quite different from, say, the meat protein of the food which is their common source. And there is a great difference between one species of animal and another in the behaviour of their characteristic proteins. What is more, the proteins of the tissues are not static once formed, but constantly receive fresh amino-acid constituents from the blood and shed their old ones to be excreted ; thus they are like a reservoir which remains at a constant level, though continually refilled and overflowing.

The breakdown products of protein which has been used as a source of energy ultimately appear in the urine, as nitrogenous compounds like *urea*, *ammonia* and *uric acid* ; and as sulphur compounds. These are derived from the food, but not entirely so ; for the body is capable of digesting and utilizing the proteins of its own tissues and in starvation it does so exclusively. The conversion of the nitrogenous part of the food protein into urea is effected in the liver by the process of *de-amination* ; the nitrogenous part of their molecules is split off as ammonia, which is transformed into urea and got rid of by the kidneys. The body does not require the bulk of this nitrogenous material, and retains only so much as is needed to replace tissue breakdown. It is the non-nitrogenous residue which is used as a valuable source of energy, and which serves to stimulate general metabolism as a bellows blows up a fire.

We must mention also the fate of certain complex proteins which go to build up the nuclei of living cells. These *nucleo-proteins* are particularly abundant in such rich and cellular foods as sweetbreads, liver, kidneys and meat. In the final breakdown of these substances, uric acid is formed and excreted in the urine ; and gout is due to an accumulation of the insoluble salts of this acid around the affected joints. The moral of which is that those with a gouty tendency should keep off sweetbreads, liver and kidneys.

Fat. The reserve or depôt fat of the body is the main source of energy in starvation. This basic fat is widely distributed, and makes up some 10 per cent of the body weight. About half is in the thick layer under the skin, some in great sheets in the abdominal cavity or as a packing round the internal organs, and a little in the intermuscular planes. Microscopically, it is seen to consist of adipose tissue, in which the connective tissue cells are distended with single large globules of fat. Chemically, it consists of the neutral glycerol salts of oleic, palmitic and stearic acids.

Fat is only added to this reserve when the food is more than the body needs for energy. Different species of animals have their own characteristic and different fats, such as liquid human fat and solid mutton fat. To a certain extent this depends on the capacity of the body to modify in its own way the fat taken in the food, but the character of the depôt fat may be altered experimentally by providing large amounts of an unusual fat in the diet. This is particularly important in milk production, as the richness of cows' milk is greatly affected by the adequacy and nature of their diet.

The carbohydrate of the diet is easily and constantly converted into fat within the body, i.e., starchy foods and sugar are fattening. Since the capacity to store reserves of carbohydrates is only some 13–14 ounces, it is clear that any excess of this substance will be turned into fat and go to swell the basic reserves. The value of the latter as an energy source lies in its high calorific value—over twice as much as that of carbohydrate and protein—and in its greater concentration, for it contains little or no water. From the physical aspect, the depôt fat insulates the body against heat loss in cold weather and buffers the organs against shock and injury ; it is also an insulator for electrical discharges and serves that purpose as a special layer around the individual fibres of the nerves. Apart from heat production, the tissues prefer to obtain their energy by the utilization of carbohydrates rather than fat ; but the latter is useful in certain situations where heavy prolonged work is done, particularly in the heart muscle.

In the utilization of fats to produce energy, the fatty acids are normally burnt completely to carbon dioxide and water. Their molecules contain a long chain of carbon atoms and the process is effected in stages as these atoms are successively split off and oxidized. During this process certain " ketone bodies " like *acetone* and *aceto-acetic acid* are formed ; but normally these are burnt in their turn and so do not appear in the urine. But if an adequate amount of carbohydrate is not being burnt at the same time, the ketone bodies are not burnt ; if the amount of fat in the diet is more than twice the carbohydrate, they appear in the urine and a toxic state of *ketosis* or *acidosis* results, usually in children. All this has been picturesquely expressed in the saying that " fat will only burn freely in the flame of carbohydrate ".

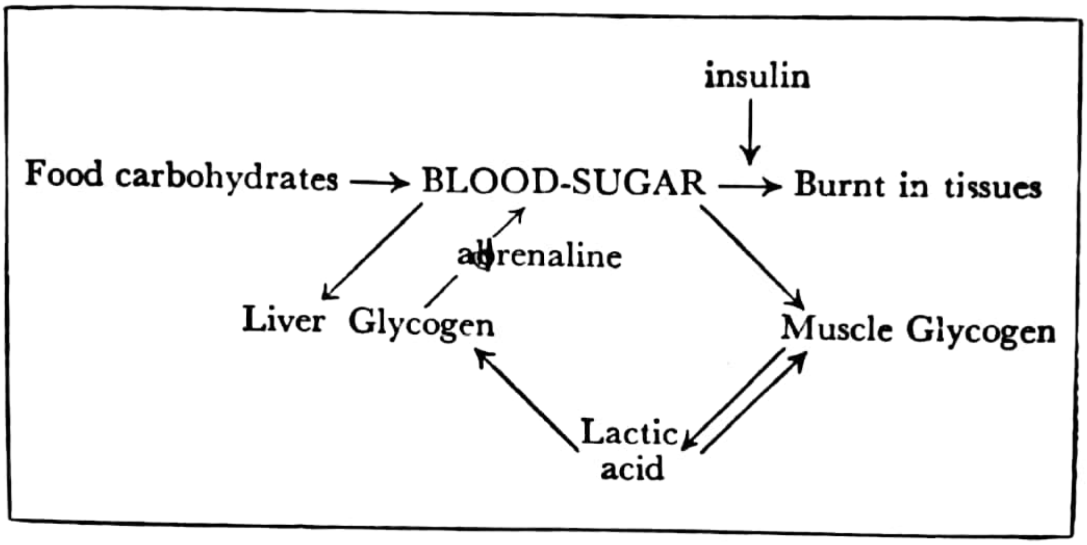
The liver plays a cardinal rôle in fat metabolism ; it contains normally some 5 per cent of fat, but more fat may appear in certain diseased conditions, for example, fatty degeneration ; and in starvation and certain forms of chemical poisoning and in many other conditions, such as the severe anaemias, the depôt fat is transferred to the liver before utilization.

Carbohydrate. The carbohydrates of the food are converted into the simple monosaccharide form, principally glucose, and absorbed as such. Glucose is found in the body as dissolved sugar in the blood lymph and tissue fluids ; and is also converted into an insoluble starch-like derivative—*glycogen*—stored as an energy reserve in the liver and in the muscles. We have earlier, in discussing protein metabolism, used the simile of a reservoir which remains at the same level though it is being constantly emptied and as constantly refilled. This applies equally to the sugar of the blood. There is a constant intake from the food, and also from the liver glycogen, which is mobilized to enter the circulation as glucose ; and there is a constant output into the tissues, where some sugar is burnt for energy and some stored in the cells as a glycogen reserve. The blood-sugar is thus in equilibrium with that of the tissues, and there is a very efficient regulating mechanism which maintains its concentration within fairly constant limits. The blood-sugar level rises somewhat after a meal, but is back to normal within two hours as the added sugar diffuses out into the tissues. This regulation is so effective that the blood-sugar remains much the same in severe starvation as after a heavy meal, and it is only exceptionally that the level rises to such an extent that some sugar spills over and is excreted in the urine.

How does this regulating mechanism work? The controlling agent is *insulin*, an internal secretion or hormone of the pancreas, a gland we have already met with in digestion. Insulin is essential to the proper utilization of sugar by the tissues, and in a normal individual is formed by the pancreas in amounts just sufficient to deal with the sugar added to the circulation from the food; its action is to keep the blood level down to normal by enabling the tissues to make use of this added sugar. Without insulin, the tissues cannot properly burn glucose, sugar is dammed up in the blood, and spills over into the urine. As a result there is relative starvation, because of the loss of this source of energy; also, as we have seen, fat metabolism is also interfered with, since sugar is not being simultaneously oxidized, and acidosis results. This combination of circumstances is the condition we know as *diabetes*; it is due to some unexplained deficiency in the secretion of insulin. The proper treatment of diabetes, therefore, depends on giving insulin artificially by injection, and on working out such a balance between the insulin given and the sugar allowed in the food that the blood level is just kept normal. In minor cases of the disease, where the capacity to utilize sugar is only slightly impaired, it may however be possible to deal with the situation merely by reducing the sugar intake in the diet. Now, since diabetes is a problem of too much sugar in the blood, due to insulin deficiency, we might expect that an excessive dose of insulin would abnormally depress the level of blood-sugar; this is in fact the case, and the consequences may be serious or fatal—feelings of acute anxiety, great hunger, pallor and sweating, convulsions, even ultimate coma and death. The same results occur in the rare condition of a tumour of one of the cell-islands in the pancreas in which insulin is formed ; so much insulin is produced by the tumour that the patient's life may depend on its location and removal. Furthermore, it is quite common for a slight over-production of insulin in otherwise normal individuals to give rise to mild spontaneous depression of the blood-sugar, marked by recurrent restlessness and hunger or even mental disturbance ; such a condition is rapidly alleviated by eating sugar or sweets.

The liver is the principal place of storage for glycogen, and it is constantly converting it into glucose, and vice versa ; it is also capable of forming glycogen from protein and fat. Just as insulin regulates the blood-sugar on the outflow side, by enabling the tissues to burn it up, so the liver regulates it on the inflow side by adding just enough from its own glycogen stores. This liver store is a reserve against starvation and can be quickly converted into soluble glucose and passed into the general circulation when necessary ; of all the reserve materials of the body this is the one most rapidly available and most easily made use of by the tissues. In its mobilization from the liver, *adrenaline,* the internal secretion of the adrenal glands, plays some part ; thus, in fear and anxiety and in apprehended or actual struggle, and in severe cold, adrenaline acts as an immediate chemical messenger to the liver and sugar is rapidly formed and poured into the blood to serve as an immediate source of energy.

The muscles of the body are the other main storage receptacles for glycogen ; this they need as an essential agent to supply their energy demands in contraction. In this process they convert the glycogen, not to glucose, but into lactic acid which enters the blood and is reconverted to glycogen either in the liver or in the muscles themselves again. Though, in fact, more glycogen is stored in the muscles than in the liver, it is kept for the particular needs of muscular exertion and is not so readily available for the general use of the body.



CHAPTER VII

EXCRETION AND TEMPERATURE REGULATION

The Kidneys and Urine

THE urine is secreted in the two *kidneys*, organs lying at the back of the abdominal cavity. From each kidney a tube, the *ureter*, carries the urine to the *bladder* in the pelvis, and it is discharged from there into the *urethra*. In the female this is a short channel which soon opens externally; in the male it is a long curved pathway traversing first the *prostate* gland and then running through the *penis*, which is also used for performing the reproductive act.

The Urine. Practically all the waste products of metabolism are got rid of, or excreted, in the urine. The only exceptions are (i) carbon dioxide, which is exhaled from the lungs; (ii) the ultimate breakdown products of bile and other digestive juices, expelled in the faeces. But it must be realized that the kidneys themselves do not form any of the wastes they excrete—they merely rid the blood of the substances formed in other parts of the body; that is to say, their essential activity is the maintenance of a constant composition of the circulating blood. In renal failure or disease this process is inefficient, the blood concentration of urea and similar wastes rises enormously, and the tissues and tissue-fluids are saturated with and poisoned by these products of metabolism. Thus, the kidneys may be regarded as a pair of filters, through which some 2 pints of blood circulate every minute, i.e., the whole of the blood in the body passes through them in 5–6 minutes.

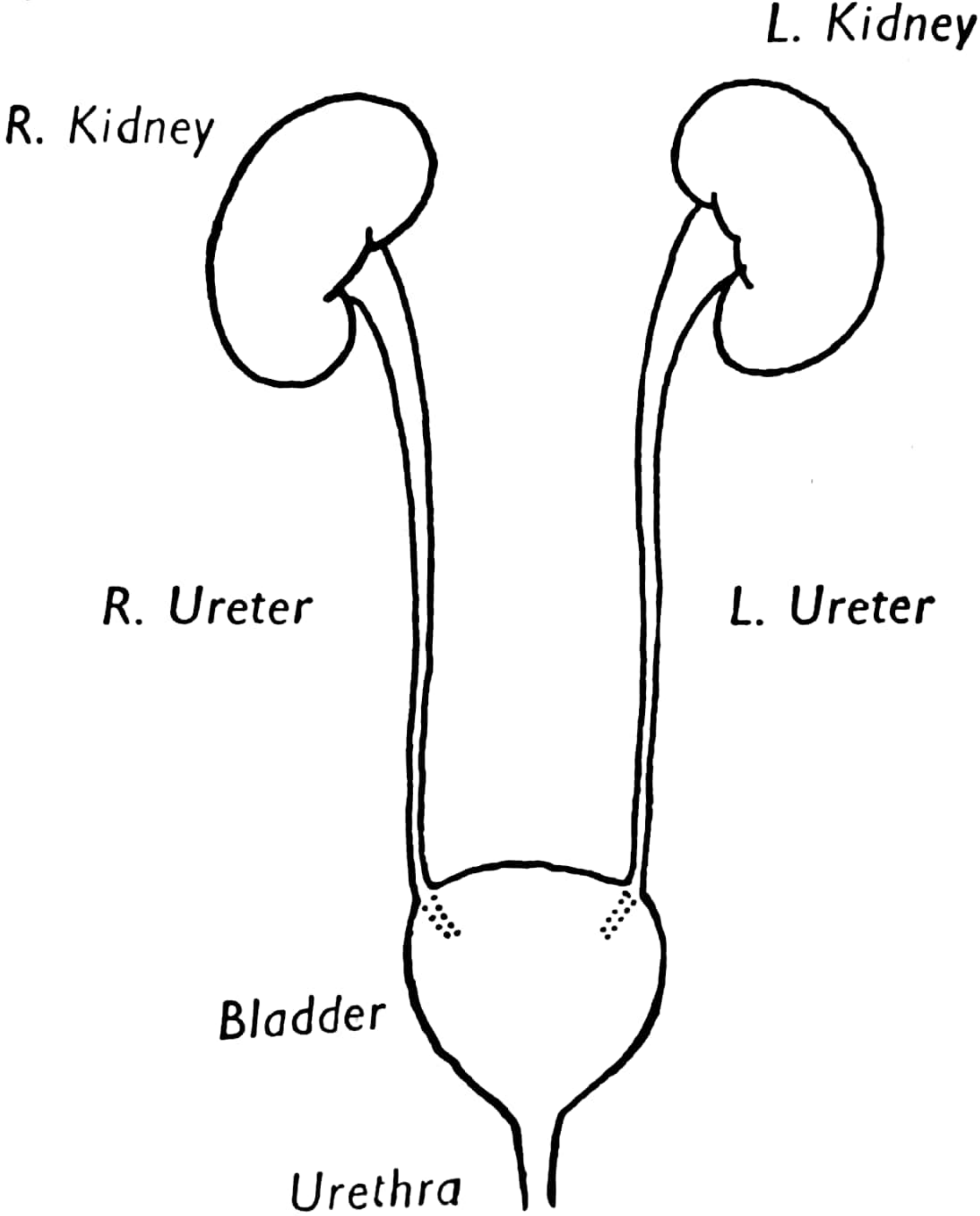


Fig. 13.—The urinary system.

The water of the urine is derived partly from the food and partly as a product of combustion in the tissues. And, while the exact composition of urine is bound to vary with the kind of food, the water intake, and the fluid loss by other channels, it remains fairly constant under average conditions. It has a clear yellow colour, paler when diluted by excessive drinking, and darker when concentrated by excessive sweating ; and it contains a certain amount of mucus derived from the lining of the urinary channels through which it has passed. It is usually moderately acid in reaction, but can be made alkaline by a vegetarian diet or by taking large amounts of sodium bicarbonate. The total output will vary with fluid intake and outside temperature—it

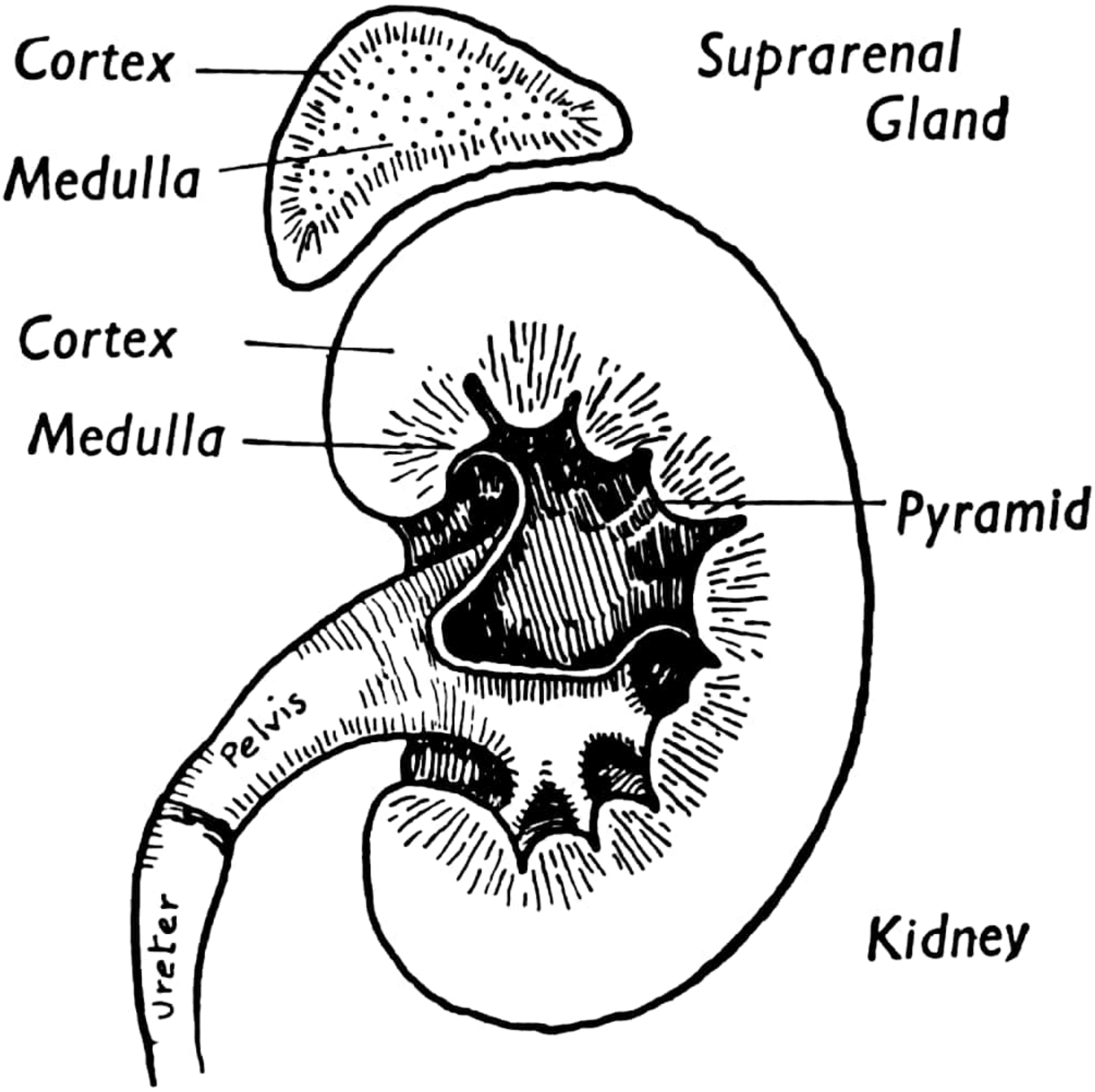


FIG. 14.—Kidney and suprarenal gland, longitudinal section.

amounts to between 1 and 5 pints every 24 hours—and its formation by the kidneys is at its lowest in sleep, and is stimulated by exertion.

The particular constituents may be grouped as organic and inorganic. The *inorganic* group includes chlorides, phosphates, ammonia, sulphates, and traces of magnesium, calcium and iron. We have seen that the ammonia is derived from the protein of the food ; the phosphates may occur in quantity and cause a heavy turbid deposit if the reaction is alkaline enough. The *organic* constituents are mostly nitrogenous end-products of protein metabolism—urea, uric acid, etc. *Urea* is the most important of these, and in urine allowed to stand it is converted by bacteria from the air into sharply-smelling ammonia, the familiar change that occurs in babies' napkins. *Uric acid* is a breakdown product of nucleo-protein and may give rise to precipitates of urate crystals. There are also various organic *pigments,* yellow urochrome and green urobilin, both derived from the bile pigments ; and pink uroerythrin.

The Formation of Urine.—To follow the process of secretion of the urine from the blood, it is necessary to understand something of the minute structure of the kidneys. Each organ is made up of several million secretory units or *nephrons,* each nephron comprising an intricately-coiled tubular system which eventually discharges with others into a larger collecting tubule draining into the central cavity of the kidney (Plate 1). Such is the functional reserve here, as elsewhere in the body, that this provision is more than adequate and a mere two-thirds of one kidney will suffice to carry out the total excretory function necessary to life.

Each tubular system is closely enveloped by a plexus of blood vessels derived from a branch of the renal artery, and it is from the waste-containing blood brought to it thus that the nephron manufactures its urine. The plexus is gathered up again into a branch of the renal vein, which removes the blood after its purification.

From the physical viewpoint, the formation of urine entails the passage of water and crystalloids from the blood capillaries into the tubules ; colloids, such as the proteins of the blood, do not appear in the urine except in kidney disease. The crystalloids involved are inorganic mineral salts and organic compounds like urea and uric acid. Now the essential feature of renal activity is that these substances are *concentrated* in the urine. The water content of urine and blood is much the same ; but there is 70 times as much urea in the urine as in the blood, 20 times as much uric acid, 30 times as much phosphate, 8 times the amount of potassium, twice as much chloride, and so on. It is obvious that to expel these substances out of the blood capillaries entails the performance of a considerable amount of work, in the physical sense, for the osmotic pressure of the proteins in the blood constantly tends to hold them back in the circulation. The driving force which overcomes this inertia is the blood-pressure itself, and is therefore ultimately derived from the pumping action of the heart. Should the blood-pressure fall below the level of the osmotic pressure of the blood proteins (some 30 mm. of mercury) as it may do in severe shock or disease, the formation of urine comes to a standstill.

But urinary secretion is not a simple physical problem, for, if it were, all the substances found in the urine would have been concentrated from the blood to an equal degree. That this is not so, that there is, for instance, 70 times as much urea in the urine as in the blood but only twice as much chloride, implies a selective action which reflects the living processes in the cells of the tubules themselves. The actual mechanism is obscure.

It may be that the material entering the first part of the tubule is a total transudate or filtrate from the blood plasma, and that a good deal of this is reabsorbed into the blood from the plexus surrounding the lower part of the tubule, except for those wastes, like urea, which are selectively retained. Alternatively, it may be that the tubule cells from the outset pick out from the blood only those substances they wish to excrete, using the driving force of the blood-pressure to reinforce this selection.

The general evidence is in favour of the first of these explanations as, the faster the circulation, the more nearly does the urine approximate to the blood plasma in composition, i.e., it is hurried along the tubules without allowing time for reabsorption of substances which properly belong to the blood.

There is also, for each particular constituent of the blood, a threshold level of concentration which must be exceeded before it appears in the urine. Thus sugar is never normally excreted by the kidneys because its threshold is rarely exceeded, save in diabetes ; on the other hand, chlorides are normal constituents of urine and only disappear in gross dehydration. In addition the kidneys play an important part in regulating the normal slight alkalinity of the blood. The urine can be acid or alkaline and thus compensate for an excessive intake of alkalies in the food or production of acids in the body.

Finally, urine formation is intimately controlled by certain of the endocrine glands, notably the adrenal and pituitary. These are particularly concerned with the water balance of the body and with the sodium and chloride ratios in blood and urine. Disease of the pituitary may lead to the output of great quantities of a pale dilute urine, a condition known as *diabetes insipidus*.

The Bladder and Micturition. Urine is propelled down along the ureters from the kidneys to the bladder by successive waves of contraction in the muscular walls of these channels. It is discharged from the ureteric orifices into the bladder in intermittent jets, every 20 seconds or so.

The bladder resembles the general plan of the internal hollow organs in being a muscular sac whose outlet below is normally closed by a tight ring of muscle, or sphincter. Bladder wall and sphincter must obviously be reciprocal in their contraction; in emptying, the bladder contracts and the sphincter relaxes to allow the efflux of urine; and in normal resting phases the bladder is relaxed to allow its gradual distension as urine collects in it, while the sphincter remains closed. *Micturition* is the expulsion of urine from the bladder to the exterior along the urethra. The control of the bladder in this respect is both voluntary and involuntary. Basically, the organ is unconsciously and automatically self-regulating, and empties itself once the internal pressure has reached a certain level. This is well shown in individuals paralysed below the waist after injuries to the spinal cord; in them the bladder continues to fill and empty because it is controlled by a nervous centre in the lowest part of the cord. When, later, we come to discuss the vegetative or autonomic nervous system (the independent regulator of such automatic bodily functions as the heartbeat and bowel movements, which are normally unconscious and independent of the central nervous system), we shall see that it consists everywhere of two parts, a *sympathetic* and a *parasympathetic* system with precisely opposite actions on glands and muscle, but always working in reciprocal co-ordination. This is so with the bladder also. The parasympathetic nerves empty it by contracting the organ and relaxing its sphincter ; the sympathetic allows it to fill by exerting the reverse action.

But there is in man, acquired in infantile development, a voluntary control of the process due to the action of the brain which can inhibit or modify the basic reflexes. There is a second sphincter surrounding the urethra itself and this is under the control of the will, so that micturition is usually a deliberate act and one aided by voluntary contraction of the abdominal muscles so as to increase the pressure expelling the urine.

The Skin

In all animals the skin functions as a protective and as a sensory agent. But in the warm-blooded creatures it has also come to play an essential rôle in the regulation of body temperature, for heat loss is almost entirely via the skin surface, with the exception of a little that occurs with the exhaled air and the excreta.

There is a continuous process of invisible or insensible loss of water by perspiration from the skin amounting to a fall of body weight of almost a pound in the 24 hours.

A great deal of this is from the palms of the hands and soles of the feet, which lose thrice as rapidly as other parts. But it must be made clear that this is not the same as ordinary sweating and not due to the action of the sweat glands, but is a simple physical transpiration of water-vapour. The sweat itself is an acid, acrid secretion, almost entirely water. But it does contain a fair amount of sodium chloride, and the amount of salt lost in this way in profuse sweating may be as much as 4 ounces a day. This loss of chloride is an important factor in the condition known as *heat-exhaustion* which occurs, for instance, in miners working underground at high temperatures. Here there is collapse, but the body temperature is normal or even subnormal ; and the condition can be prevented by adding a little salt to the water drunk during work. Note that this is not the same as true *heat-stroke*, which will be discussed in a moment.

The sweat also contains some urea, derived from the blood ; and occasionally, in severe kidney failure, the alternative excretion of urea in this way covers the skin with a sort of hoar-frost of urea crystals.

The action of the sweat glands is controlled by the nervous system, and this is set to regulate, not the amount of water lost (for this is taken care of by the kidneys) but the body temperature. That is, it depends on the difference between the internal and external temperatures ; on the rate of heat production in metabolism ; and also on the humidity of the outside air, which may act as a serious limiting factor, for unless continuous evaporation of the liquid sweat is possible the process will be interfered with. A moving current of air is another factor which encourages sweating. In practice, the stimulus to sweating is a minimal rise of body temperature by a third or half a degree, which sets the mechanism in action. Strangely enough, the palms and soles are not stimulated by a rise in internal body temperature ; but they are intimately affected by the general nervous and emotional state—the so-called " psychic sweating ".

Other Functions of the Skin. A certain amount of absorption may occur through the intact skin, but only of substances made up as an ointment with a fatty basis ; watery solutions cannot permeate the outer layers. To a very minor degree the skin is also an accessory organ of respiration, acting as a surface for the excretion of carbon-dioxide. And the skin is of some importance as a storage organ, particularly of fat and of water. We have already seen that the subcutaneous fat makes up some 50 per cent of the total fat reserve available for calls in starvation ; but the loose connective tissue of this region is also a convenient depôt for excess water. When this amount becomes excessive, over 10 per cent of the body weight, as occurs in heart failure and some forms of kidney disease, it produces an obvious boggy swelling of the skin, which can be indented with the finger. This is known as *oedema.* It is seen also in a variety of other conditions, such as the famine-oedema of starvation victims, in whom the blood proteins have fallen so low from malnutrition that their osmotic pressure is no longer capable of preventing the outflow of water from the capillaries into the tissues. Oedema is usually influenced by gravity, i.e., it is most obvious in dependent parts such as the ankles and feet.

Temperature Regulation

This is a convenient place to consider the general question of the regulation of body temperature. In cold-blooded animals the body temperature closely parallels that of the environment. In warm-blooded creatures the body is maintained at a constant temperature though the outside level may vary enormously ; a particular instance of the general physiological principle of the maintenance of a constant internal milieu. The body can be kept warmer than cold surroundings by reason of the heat produced in the oxidative processes of metabolism ; and colder than very hot surroundings by the power of controlled heat loss in sweating. Normally, therefore, a constant body temperature implies an exact balance between heat production and loss ; and the latter is a function of the surface area and is, therefore, relatively much greater in children, whose surface is so much larger than in adults in proportion to body weight.

The average body temperature taken in the rectum is 37·5° C., in the mouth 36·5° C., and in the armpit 35·5° C. But it must be understood that the idea of a standard internal temperature is only conventional, for two reasons. First, there is a daily fluctuation over one or two degrees, highest in the early evening and lowest in the small hours of the morning; and it is interesting that this is reversed if the individual is made to work at night and sleep by day. This fluctuation has superimposed on it, in women, characteristic variations at different times of the menstrual cycle. Second, organs like active muscles are hotter than others like the skin, which is losing heat; so that there is really a temperature gradient rising from the surface to the interior over several degrees.

The regulation of body temperature may obviously be effected by changes in the rate of heat production or in the rate of heat loss; usually both are simultaneous.

Regulation of Heat Production. Though all the tissues produce heat, the muscles predominate because there is always some contraction occurring, as a part of the machinery for maintaining posture; and the liver also is an important heat-forming organ, as a result of its tremendous metabolic activity. With any change in the temperature of the environment heat production is increased or decreased so as to compensate. Thus in response to cold, there is more muscular activity, which may amount to violent shivering; and at the same time liberation of adrenaline from the adrenal glands stimulates metabolism generally and sets free glycogen from the liver to be burnt in the tissues. External warmth reverses these changes.

It must be realized that these changes are due to the control of the nervous system, which plays on the muscles, and of chemical messengers like adrenaline.

Left to themselves, the tissues would behave like those of cold-blooded animals, increasing their activity and producing *more* heat as the outside temperature rises; and this is what actually happens, with possibly fatal results, when the central regulating mechanism fails, as in heat-stroke.

The Regulation of Heat Loss. Heat may be lost by *conduction*, *convection*, *radiation*, or by *evaporation* from the body surface. Of these, *conduction* is of little importance since the skin and subcutaneous fat are such good insulators. *Convection* is more important; the layer of air immediately adjacent to the skin is warmed, and then rises, and each warmed layer of air is successively replaced by colder layers which are warmed in their turn; and this process is obviously greatly accelerated by external air currents. *Radiation* is also of significance since the body surface happens to be, from the physical viewpoint, a very efficient radiator indeed.

Finally, *evaporation* varies greatly with circumstances. At low temperatures there is only the insensible vapour loss; sweating begins at an air temperature of 29–30° C.; and if this reaches body temperature, sweating and evaporation become the only method of heat loss, since convection and radiation must obviously come to a standstill when there is no longer any temperature gradient between the skin surface and the environment. The cooling effect of evaporation is due to the fact that a considerable amount of energy is needed to convert the water of sweat into water-vapour, and this energy is abstracted from the heat of the body.

Under average conditions, a clothed adult effects about two-thirds of his heat loss by convection and conduction, and rather less than a third by evaporation. In addition to these purely physical considerations, heat loss is controllable to some extent by certain physiological activities. Most important of these is the possible fluctuation in the calibre of the small blood capillaries of the skin. These may open up widely to produce a flushing, or *vasodilatation*, which increases the surface temperature and so accelerates heat loss because of the steeper gradient to the outside level. (It also improves the actual conducting power of the skin by raising its fluid content.) Or they may shut down, to produce a cold pallid skin surface—*vasoconstriction*—with a reduced rate of heat loss. This fluctuation may be enormous ; the maximum blood supply to a patch of skin may be 50 times the minimum. And these changes are under the remote control of the central nervous system, via the sympathetic (vasoconstrictor) and parasympathetic (vasodilator) nerves already referred to.

However, this mechanism, sensitive as it is, ceases to operate when the outside temperature reaches the level at which sweating and evaporation become significant. And the mechanism of sweating and evaporation is so efficient that a man can easily sustain exposure to outside temperatures which will cook a piece of meat in a few minutes, provided the atmosphere be *dry*, so that evaporation is unhindered. If the air is saturated with water-vapour, or if—which amounts to the same thing—the individual is born without sweat glands and is unable to sweat, his temperature will rise rapidly with possible death from heat-stroke. In this condition, which is not necessarily due to direct exposure to the sun, there is actual damage to the vital centres of the brain ; the whole heat-regulating mechanism breaks down and the body temperature continues to rise until death occurs in coma or convulsions. This is quite separate from heat-exhaustion, which we have already referred to as following excessive sweating, with chloride loss, *fall* of temperature and circulatory failure.

The ultimate regulation of body temperature is fundamentally nervous. Though sweating and skin blood-supply are immediately managed by the autonomic nervous system, the ultimate control is from special centres in the middle and hind parts of the brain. These act in two ways. They are very sensitive to minute changes in the temperature of the blood brought to them by the circulation, and so react as to restore it to its previous level. And they are also sensitive to the *nervous* stimuli that a hot or cold application produces on any part of the body surface. For the skin is provided with special heat and cold receptors, which are greatly modified nerve endings, those for cold being rather the more sensitive.

The heat-regulating centres effect their results by the ways we have already discussed ; by producing shivering, sweating, more or less heat production and muscular activity, changes in metabolism, vasoconstriction and vasodilatation, and so on. The important point is that, like the governor of a machine, the mechanism is usually *set* at a certain level and reacts to maintain that level under all changes of outside circumstance. But if it is shifted by some general upset the setting may change, and this is, for instance, what happens in fevers where the gearing is adjusted upwards a few degrees.

The effect of *clothing* is mainly to protect from either extreme of temperature by providing a good insulating layer, whose efficiency is increased by the amount of air entangled in the interstices of the material and between its layers ; the effect is therefore greater with several light garments than with one thicker one. But clothing considerably cuts down the radiating power of the body ; and its capacity for permeation with moisture is responsible for the very chilling effect of a cold damp climate.

CHAPTER VIII

THE BLOOD

THE blood is the fluid medium which pervades all parts of the body, conveying food and oxygen to the tissues and carrying off wastes to be excreted. It varies in colour between the purple of venous blood and the bright red found in the arteries, according to its degree of oxygenation. Microscopic examination shows that its uniform texture is only apparent; for there are myriads of *corpuscles* of different kinds suspended in the fluid element or *plasma*. Corpuscles and plasma occupy an approximately equal volume, and can be largely separated from each other by centrifugal force. In a centrifuge the corpuscles are thrown to the bottom of the tube, leaving the clear plasma above.

Corpuscle
&
Plasma

After a severe haemorrhage the fluid loss is rapidly made good by the entrance of water into the circulation from the body reserves; as a result there is considerable dilution and a much lower corpuscle count than normal. The reverse occurs in severe shock and in dehydration, where plasma leaks out into the tissues, leaving a very thick and viscous concentration of corpuscles in the blood vessels.

The total volume of blood in the body is easily estimated by injecting a known amount of dye into the circulation and noting the extent to which it becomes diluted; the average blood volume is 9–10 pints.

The blood is slightly alkaline in reaction, with a pH of 7·4. But if we try to neutralize it with acid, considerably more is required than would be assumed from this modest degree of alkalinity ; and this is because there is a considerable loosely-tied alkali reserve of sodium bicarbonate functioning here, as in other tissues, as a buffer agent resisting any change in chemical reaction. Only when this reserve is greatly reduced can true acidosis develop, and this is exceedingly rare.

The *plasma* is a clear pale yellow fluid, containing some 10 per cent of solids, most of this being protein, and a certain amount of salts, particularly sodium chloride. There are also some sodium bicarbonate, phosphates, potassium, etc. ; and also representative products of the stages of metabolism of all the different classes of foodstuffs—glucose, urea, amino-acids, fats, and so on. The proteins of the plasma are coagulable, and one of them, fibrinogen, is concerned exclusively with the clotting of blood. The others, albumin and globulin, are responsible for the considerable osmotic pressure of blood.

Clotting. Normal blood clots a few minutes after being shed, becoming completely solid. The jelly-like clot is composed of a meshwork of threads of a substance called *fibrin*, derived from the fibrinogen of the plasma ; this meshwork soon contracts to a much smaller bulk, squeezing out a straw-coloured fluid, the *serum*, which is what is left of the plasma after the loss of its fibrinogen. Serum and plasma are largely, therefore, but not entirely, identical.

BLOOD (PLASMA + CORPUSCLES) →
CLOT (FIBRIN + CORPUSCLES) + SERUM.

Clotting is a complex mechanism requiring the presence of calcium salts, and prevented by substances like sodium citrate which precipitate calcium. But the process also has to be activated by substances derived from the tissues, a means of securing clotting after wounds which tear the tissues and liberate their juices.

If blood is shed with a minimum of damage and received into a perfectly clean or waxed vessel, it remains fluid for a considerable time. Certain other facilitating agents are also necessary ; one of these is formed in the liver, and the well-known haemorrhagic tendencies in liver disease and jaundice are due to its absence. Another essential factor is constitutionally absent in " bleeders " or haemophiliacs, victims of a disease which is transmitted to male descendants by the female members of the family, themselves immune. Finally, certain chemical substances have been recently isolated from the liver and from spoiled clover which greatly delay the coagulation of the blood, or even abolish it. And these have been found of use in surgery in such operations as the repair of injured blood vessels, where it is important to keep the new channel free of clot.

The *corpuscles* of the blood include the *red corpuscles, white cells,* and the smaller *platelets* ; their relative numbers are as follows :

red corpuscles .	5½ million per cubic millimetre.
white cells . .	4000–10,000 per cubic millimetre.
platelets . .	150,000–350,000 per cubic millimetre.

The Red Corpuscles are cells which have lost their nuclei, biconcave discs which appear narrow-waisted when seen in profile. They are little more than envelopes containing the respiratory pigment of haemoglobin, which gives to each individual cell a yellow colour and to large aggregations the typical red. This splitting of haemoglobin into innumerable little packets vastly increases the surface area at which the interchange of oxygen can occur, for the total area of the red cells is somewhere between 1000 and 2000 times that of the body itself.

We have already seen that the red corpuscles are peculiarly sensitive to changes in the osmotic pressure of the medium in which they float ; and that an increase in osmotic pressure makes them shrivel up by withdrawing water, while a weaker solution allows them to swell up and burst, when the pigment is set free and the blood is said to be *haemolysed.* The natural fragility of red cells is pretty constant, except in certain individuals where they rupture very easily, and these are prone to jaundice from the liberation into the circulation of an excessive amount of pigment.

Haemoglobin itself is a complex protein linked to a chemical grouping containing iron, which is responsible for the colour. It can be obtained in crystalline form and its particular value lies in the ease with which it combines loosely with oxygen (in the lungs) to form bright red oxy-haemoglobin, and the ease with which this oxygen is given up to the tissues, leaving the purple reduced haemoglobin. (It may be convenient to emphasize here that carbon dioxide is not carried to any great extent in the corpuscles, but is dissolved in the plasma ; this will be discussed again in Chapter X.)

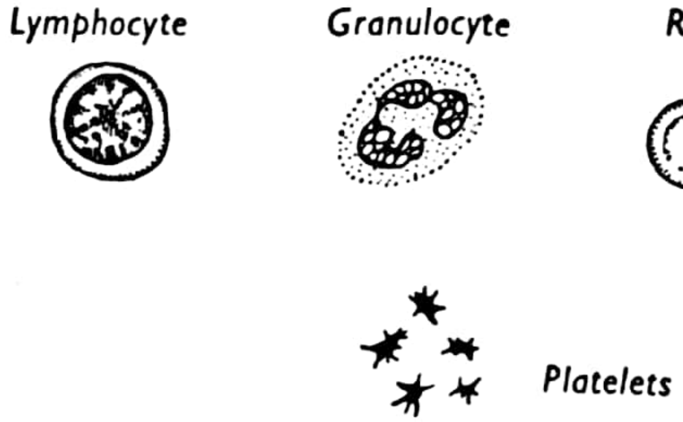


Fig. 15.—The different types of blood corpuscle.

The red cells are formed, before birth, in the marrow, liver, spleen and lymph glands. After birth the marrow is their only source, save in exceptional circumstances.

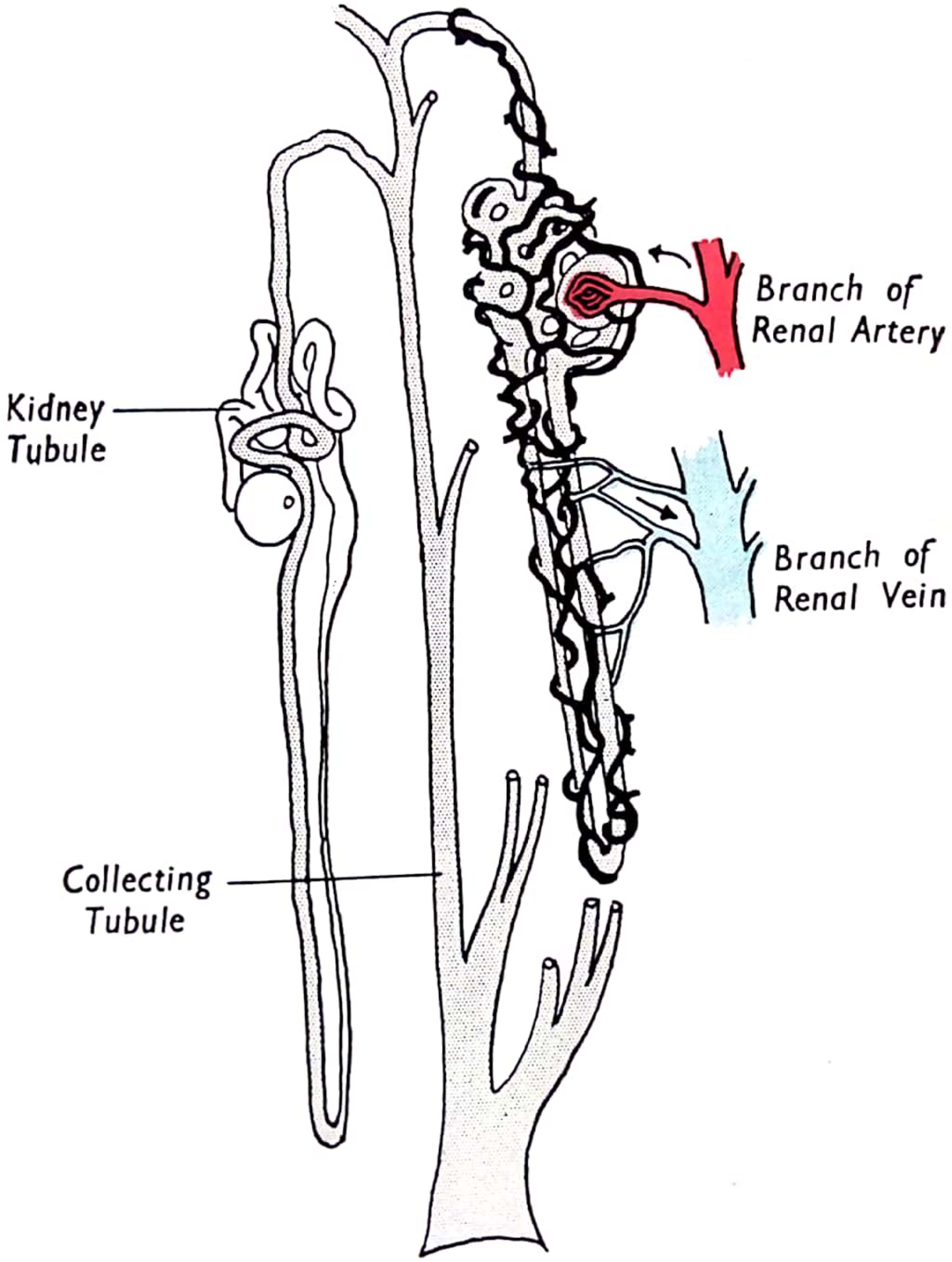
The corpuscles represent the end of a line of development from specialized cells which eventually lose their nuclei ; but an occasional intensive demand on production in response to haemorrhage or anaemia results in the appearance of abnormal nucleated forms in the blood. This continuous process of formation is in equilibrium with the process of destruction, and the average life of a red cell is some 3 months.

It is conventional when estimating the efficiency of an individual's blood in the transport of oxygen, and in calculating any degree of anaemia, to take as the 100 per cent standard a content of 14·8 grammes of haemoglobin in 100 cubic centimetres of blood. In fact, the haemoglobin level of healthy men is as much as 110 per cent, and of women 102–105 per cent. It is also conventional to take the 100 per cent standard number of red corpuscles as 5,000,000 per cubic millimetre ; and it is therefore possible to express the relative haemoglobin content of the individual corpuscle as the figure

$$\frac{\text{percentage haemoglobin of the standard figure}}{\text{percentage red cells of standard number}}$$

This is the *colour index* and is of course equal to 1 in the individual with 5,000,000 red cells per cubic millimetre, and 100 per cent of haemoglobin.

Anaemia occurs when the haemoglobin falls below 100 per cent, and may be due to fewer red cells, a reduced amount of haemoglobin per cell, or both ; or even, as in pernicious anaemia, to a smaller number of cells each of which actually contains *more* haemoglobin than normal. Ordinary anaemia is due to a lack of iron, which is essential to the formation of haemoglobin ; the cells are paler and smaller, the colour index less than 1, the haemoglobin may fall to 50–60 per cent,



The Plate shows two kidney nephrons—the microscopic coiled tubes in which the urine is formed—draining into a common collecting tubule. The blood vessels which carry blood to and from each tubule for purification are shown on one side.

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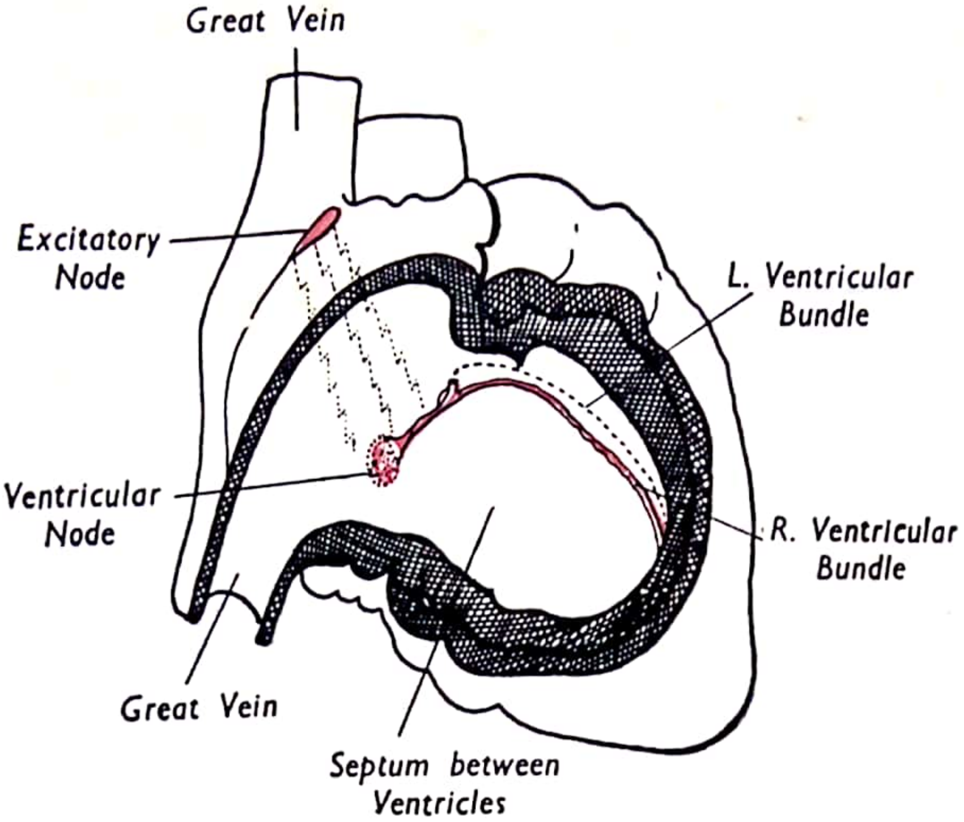
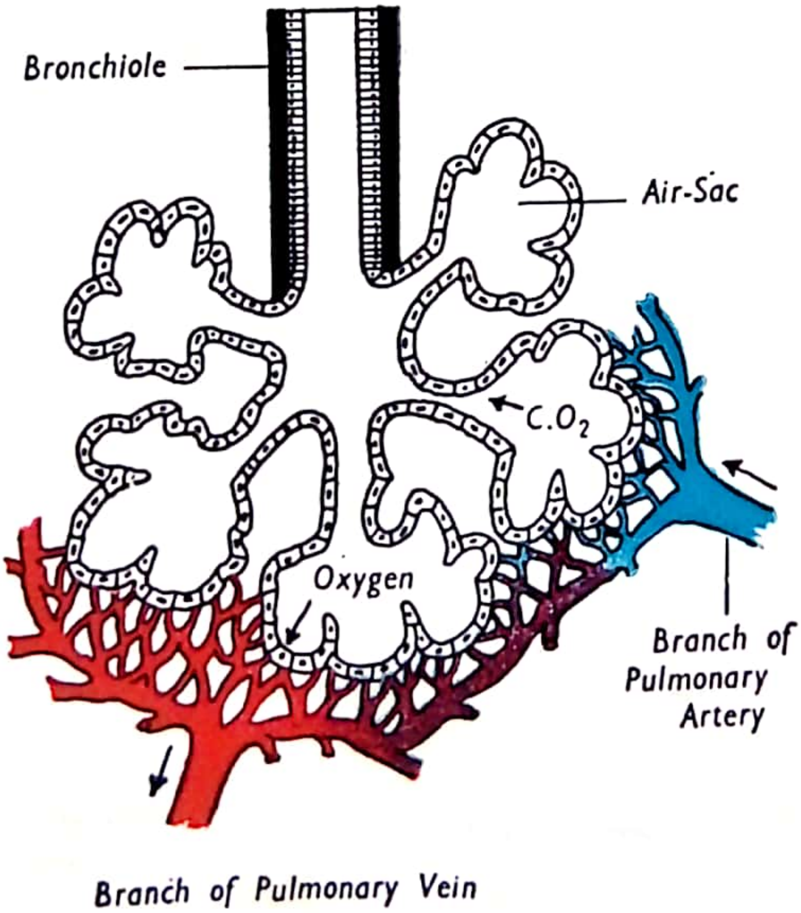


The right side of the heart opened to show the mechanism which excites regular contraction of the muscular chambers. The stimulus begins at the excitatory node and spreads to the ventricular node, whence it is conveyed by a special bundle of fibres to each ventricle.

(Adapted from Starling's *Principles of Human Physiology*.)



The interchange of respiratory gases in a cluster of air-sacs of the lung.

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and this is known as *hypochromic* anaemia because the red cells contain less colouring matter than usual. In pernicious and related anaemias there are larger and redder cells than usual with a colour index greater than 1, but far fewer of them ; the haemoglobin may fall to 15–20 per cent, and the condition is an example of *hyperchromic* anaemia, i.e., more colour than usual in the red cells. A large number of chemical factors are essential for the proper maturation of the red cells and filling them with the right amount of haemoglobin ; and lack of any one of these factors may give rise to a different type of anaemia. They include iron, copper, vitamin C, and thyroid hormone ; and one of particular importance which is formed in the stomach as the product of combination of an intrinsic factor in the gastric secretion and an extrinsic factor derived from the food. This substance is stored in the liver ; its deficiency is the cause of *pernicious anaemia* (which occurs in people whose gastric secretion is defective) ; and it can be cured by the administration of liver or stomach extract.

The obvious results of anaemia are : pallor of the skin and mucous membranes which is, however, difficult to estimate casually ; and breathlessness due to the lowered oxygen-carrying capacity of the blood, which makes extra demands on the heart and may result in cardiac failure. The body is capable of considerable adjustment to even severe anaemia if its onset is gradual ; it may be possible to walk about in comparative comfort with a haemoglobin as low as 40 per cent if the cause is a very chronic one, but a rapid fall to 60 per cent from haemorrhage may produce severe breathlessness.

The White Blood Cells. These include two main varieties. The *granulocytes*, making up some 75 per cent of the white cells, are capable of independent movement in the blood-stream and within the tissues, and can swallow up dead bacteria and foreign particles. They have a nucleus of several lobes, and are intimately concerned with the process of inflammation. For, at the site of injury or infection, these cells ooze through the walls of the capillaries and assemble in great numbers in the affected part to overcome the micro-organisms and remove waste material and the debris of repair. If, instead of incorporating and digesting the bacteria, they are themselves killed, their dead bodies form a large part of the pus that results. The granulocytes are formed in the marrow and, like the red cells, have only a comparatively short life.

The *lymphocytes*, some 25 per cent of the total white count, are smaller, with a single large nucleus nearly filling the cell. They are formed in the numerous lymph glands of the body, from which they enter the blood-stream and are concerned with the development of immunity against infection, though not in themselves mobile or capable of an active part in antibacterial warfare.

The Platelets are tiny bodies, much smaller than the red or white cells, with irradiating spicular processes giving them some resemblance to an asterisk in appearance. They are not true cells and have no nucleus, but are fragments of bone-marrow cells shed into the circulation. Their main function is to assist in the clotting of the blood, where each acts as a focus for the deposition of fibrin.

Blood Groups. It has already been mentioned that human tissues and fluids are sensitive to foreign proteins and react, sometimes violently, against them. If in solution, this reaction causes their precipitation. This applies as much to the blood as to any other tissue; thus human plasma mixed with animal blood causes the red cells of the latter to clump together in sticky granular masses like grains of pepper, a process spoken of as *agglutination.* It is for this reason that animal blood is useless for transfusion, the agglutination of the transfused cells blocking the vessels in the vital parts, while the debris after their destruction obstructs the secretion of urine in the kidneys.

Unfortunately this same sensitivity exists, not only as between man and animals, but as between one individual and another if they happen to belong to different blood groups, and may produce the same disastrous results. Within the same group transfusion is quite safe ; outside this, only certain combinations are safe and these must be rigidly adhered to. There are four main groups, designated as O, A, B, and AB. Their relations to each other from the aspect of compatibility in giving or receiving a blood transfusion are indicated in the following table : it will be noted that they are complicated in virtue of the fact that it may be quite possible for a member of one group to donate blood to another, though it would be fatal for him to receive from the latter.

Group	*Can give blood to :*	*Can receive blood from :*
O	O, A, B, AB	O
A	A, AB	O, A
B	B, AB	O, B
AB	AB	O, A, B, AB

It will be noted that Group O is safe for everybody and therefore a universal donor ; and fortunately this is found in some 40 per cent of the population. Group AB, safe for donation to its own group only, is capable of receiving blood from anybody and is in the lucky position of being a universal recipient ; but it only includes some 2 per cent of all individuals.

The blood groups of persons are transmitted to their children by the ordinary laws of inheritance and are therefore of value in cases of disputed paternity, though the evidence they provide is negative only, i.e., it is only possible to say that a certain person could *not* have been the father of a child, when the latter's blood contains a special factor which is not present in that of the accused or of the mother.

A recent development of some importance has been the discovery that the cells of certain individuals contain a special agent known as the Rh factor because of its similarity to a component of the blood of the Rhesus monkey. Most people (about 85 per cent) have this factor, and these are Rh positive and can marry and have children normally. But if an Rh positive man marries a woman of the Rh negative minority, and she becomes pregnant, the developing child receives the Rh factor from its father and this excites a serious antagonistic reaction in the mother. Substances are formed in her blood which pass to the womb and enter the child's circulation, causing extensive destruction of the latter's red corpuscles; and the infant is born dead or with serious anaemia or jaundice. Recent work has shown the possibility of saving some of these children, once the condition is suspected after a history of previous still births and after tests on the parents, by replacing the infant's blood as soon as possible after birth with that of a safe group.

CHAPTER IX

THE CIRCULATION

THE circulatory system is essentially a closed circle of tubing round which the blood is propelled by the contractions of the muscular heart. Blood is driven into the *arteries*, thick elastic tubes which by their recoil aid the distribution of the blood to all parts. The arteries divide into smaller branches in their course to the organs and limbs and finally break up into a meshwork of fine *capillaries*—microscopic thin-walled vessels which pervade every tissue of the body except the cornea

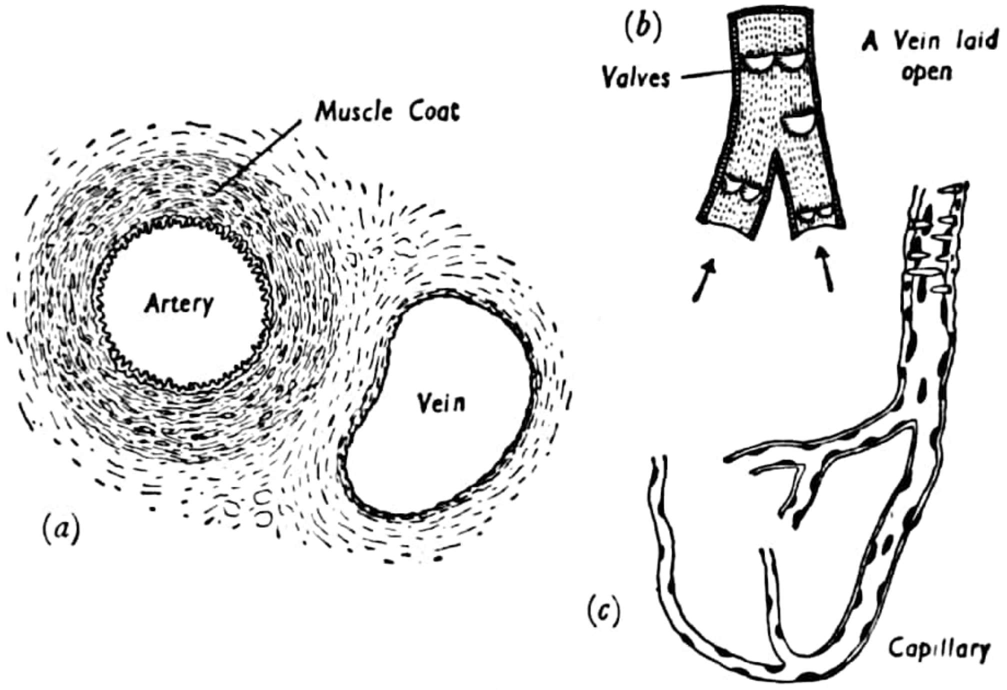


FIG. 16.

(*a*) Cross-section of an artery and vein shows the much thicker muscular coat of the former.

(*b*) Vein slit open longitudinally showing the valves with their pockets directed towards the heart.

(*c*) A capillary with its delicate walls.

of the eye and the outer layer of the skin. This meshwork joins up again to form small *veins*, which become large venous trunks as they travel centrally towards the heart. The veins are thin-walled, have no pulse, and contain valves to prevent any backward flow of blood.

Now there are in fact two quite separate circulations: a *systemic* circulation, concerned with the body as a whole and driven by the left side of the heart; and a *pulmonary* circulation, concerned with the passage of blood through the lungs and driven by the right side of the heart. The two sides of the heart are quite shut off from one another; and each side has an upper chamber or *auricle* receiving blood from the great veins, and a lower chamber or *ventricle* discharging blood into the great arteries. Stale venous blood from the body enters the right auricle, passes to the right ventricle, and is expelled through the pulmonary artery to traverse the capillaries of the lungs. Here it is aerated, receiving fresh oxygen from the air in the air-sacs and giving up carbon dioxide to be exhaled. The fresh blood returns from the lungs in the pulmonary veins to the left auricle of the heart, then down to the left ventricle, and is discharged into the great artery of the body, the aorta, which supplies the head, trunk and limbs through its branches. In the body tissues the blood is rendered dark and venous and is collected up ultimately into two great veins, the *superior vena cava* draining the head and arms and the *inferior vena cava* draining trunk and legs.

Note that, whereas the arteries of the body contain bright blood, and the veins dark, the reverse is inevitably the case for the pulmonary vessels, because the lungs are concerned with reversing these chemical states of the blood.

✓ Then there is a special arrangement of the abdominal vessels which must be noted. Whereas the veins leaving

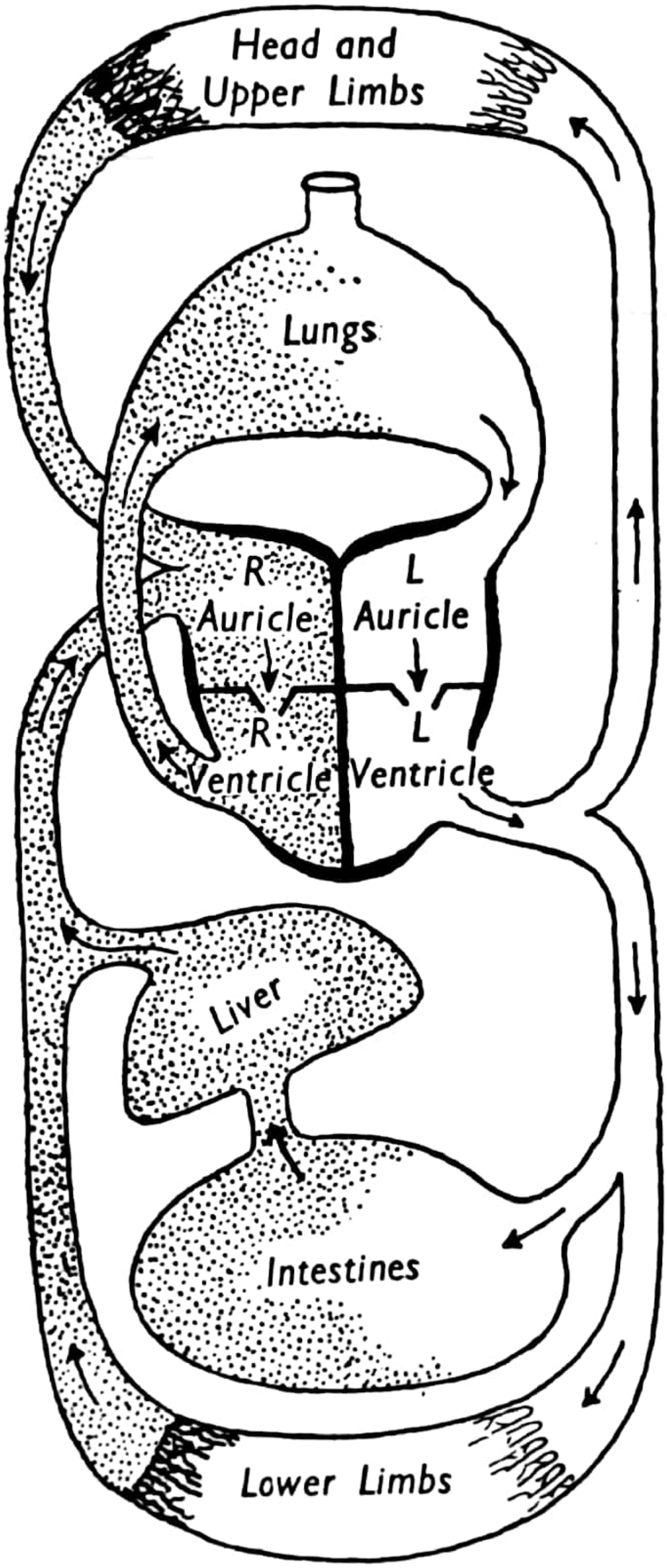


FIG. 17.—A diagram of the circulation of the blood.

most structures pass directly to the heart, those from the stomach and intestines enter another organ, the liver, where they break up into a second set of capillaries so that the blood is filtered through the liver before reaching the heart. This is, as we have seen, to secure that the liver utilizes and stores foodstuffs absorbed from the bowel, and this arrangement is known as the *portal system.*

Physiological Features of the General Circulation. The circulation is everywhere a closed system, and though the calibre of the blood vessels varies enormously, the blood as a whole never escapes into free contact with the tissues. The motive power of the circulation is the pumping action of the heart, which acts as a boosting mechanism set in the middle of a pipeline, for it receives blood from the veins at very low pressure and transmits it to the arteries at a very high one. When the blood eventually leaves the arteries to circulate through the tissues in delicate thin-walled capillaries, the plasma can diffuse through to mix with the tissue juices which bathe the cells and form the lymphatic fluid.

There is therefore a pressure gradient in the circulatory system, from the high level in the great arteries of the body to an intermediate point in the capillaries and still lower to the pressure in the veins, which may be zero ; in fact, the circulation in the veins is largely dependent on such outside assistance as the sucking action of respiration, which draws blood into the chest and heart, and on the contraction of the muscles which surround the veins in the limbs. Thus on walking the leg veins are constantly being emptied by the milking action of the muscles ; and the simple valves in the veins prevent any reflux and direct the flow towards the heart.

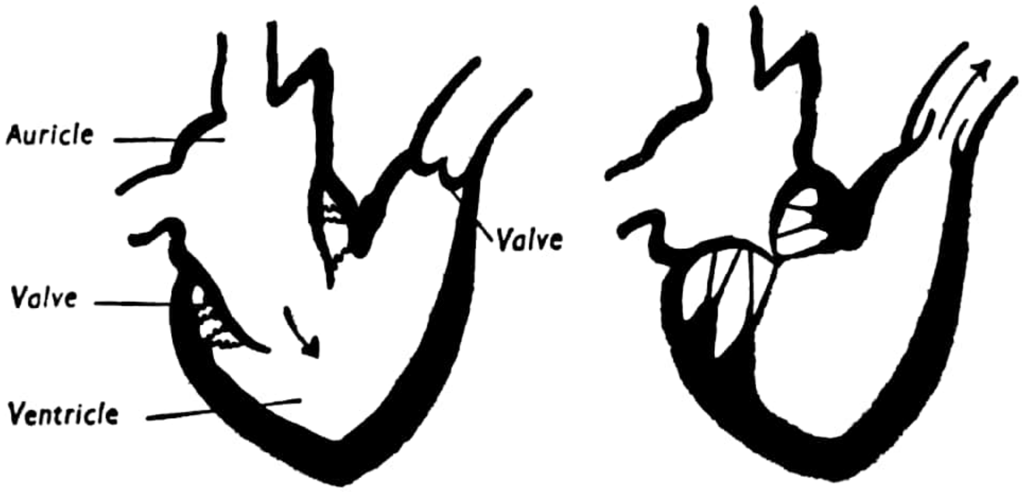
This difference between the veins and arteries is reflected in their structure ; the veins are thin-walled with little muscular or elastic tissue, whereas the arteries have thick coats with a good deal of muscular tissue and elastic fibres. This allows the arterial side of the circulation to act as a distensible and elastic distributing system, with a recoil to the heartbeat which is transmitted away from the heart as far as the capillaries to produce the pulse as we see it at the wrist or temple. Moreover, the contractile power of the arteries serves to maintain a higher blood-pressure at a greater distance from the central pump than would a system of simple inelastic tubes. And, in addition, the smaller arteries and arterioles can exert a selective action on the local circulation in particular regions, by constricting or dilating to shut off or increase the blood flow to a certain organ or muscle or area of skin. This is in marked contrast with the veins, which form an inelastic reservoir which may become a stagnant pool if their valves become inefficient or if the heart begins to fail.

As the arteries divide, the cross-sectional area of their branches is greater than that of the parent stem until, when we reach the capillaries, the total sectional area or " capillary bed " may be almost 1000 times that of the aorta, the great artery, leaving the heart. This enormous difference in area is another aspect of the progressive fall in blood-pressure as the arterioles branch into the capillaries ; and, when all the capillaries of the body are widely dilated, as in shock after injuries, the general level of blood-pressure falls very seriously, in the great arteries as well as the smaller vessels.

The Heart. Although we have compared the heart to a pump it is far more efficient than any manufactured by man, for it continues to beat regularly and without interruption, rarely missing a beat, for 70 years with a rest interval never longer than a fraction of a second.

This power of rhythmic contraction is inherent in the organ itself and independent of nervous control, for it continues when the animal organ is experimentally removed from the body and kept under suitable conditions ; chicken hearts have been kept contracting in fluid culture media for many years.

The heart beats at the rate of some 70 times a minute at rest in the adult ; more rapidly in children, and as



Relaxation Diastole

Systole Contractio

FIG. 18.

In relaxation or *diastole* the blood flows into the ventricle from the auricle through the open valve between.

In contraction or *systole* the valve is slammed shut as the ventricle expels its blood into aorta or pulmonary artery.

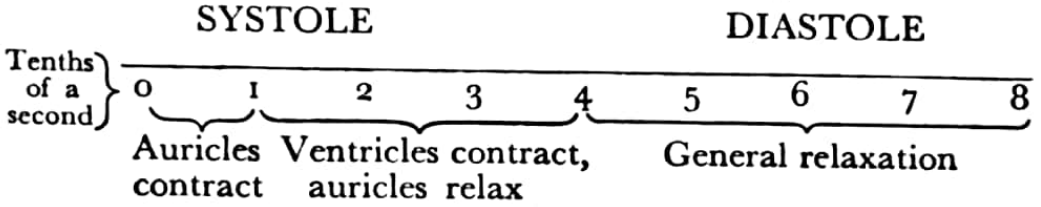
fast as 150 in the developing child in the womb. Contraction of the organ is known as *systole*, relaxation as *diastole*. Each beat begins as a simultaneous contraction of both auricles expelling blood into the ventricles ; this is followed by ventricular contraction which throws the second blood into the great arteries. This regular cycle lasts 8/10 eight-tenths of a second, of which auricular contraction makes up one-tenth, ventricular contraction three-tenths, and complete relaxation or diastole the remaining four-tenths. During diastole the auricles act as

atria ventricular contraction — Systole

4/10 complete relaxation — diastole

4/10

passive receptacles draining the blood from the great veins; and since they contract a little before the ventricles, while the latter are still relaxed and offering no resistance to the influx of blood, the auricles have not a great deal of work to do and are relatively thin-walled. On the other hand, the ventricles have the whole resistance of the peripheral circulation to overcome, notably the elasticity of the arteries, and are correspondingly thick-walled and powerful. Since the right ventricle is concerned with driving the blood through the lungs only, it has rather less work to do than the left, which deals with the circulation of the whole body; and its wall is therefore only a quarter as thick.



The regular and rhythmical sequence of events in the cardiac cycle is due to the existence within the organ of two little foci of primitive and sensitive connective tissue which act as the switches that fire off each contraction. These *nodal points* are stationed one at the junction of great veins and auricles, one at the auriculo-ventricular junction. They are connected with the heart muscles as a whole by a special cable of fibres which runs down the length of the septum between the two halves of the organ, giving a main branch to right and left side. The heart is quite soft and flaccid in the relaxed period of diastole; when it contracts it becomes thick and cone-shaped and transmits an impulse which may be seen and felt to the front of the chest on the left side. This is the *apex beat* and is found a little below the left nipple, in the space between the fifth and sixth ribs. If one listens with a stethoscope, or even with the unaided ear. over this point it will be found that two characteristic sounds go with each beat, coming very closely after each other and repeated after the diastolic pause. These may be graphically represented as follows :

.....lubb, dupp......lubb, dupp.........lubb, dupp......

and are both associated with ventricular contraction. The first is the slamming shut of the parachute-like valves which prevent any reflux from ventricles into auricles. The second occurs at the end of ventricular contraction when the valves at the mouths of the great arteries fall together to prevent any backflow into the ventricles.

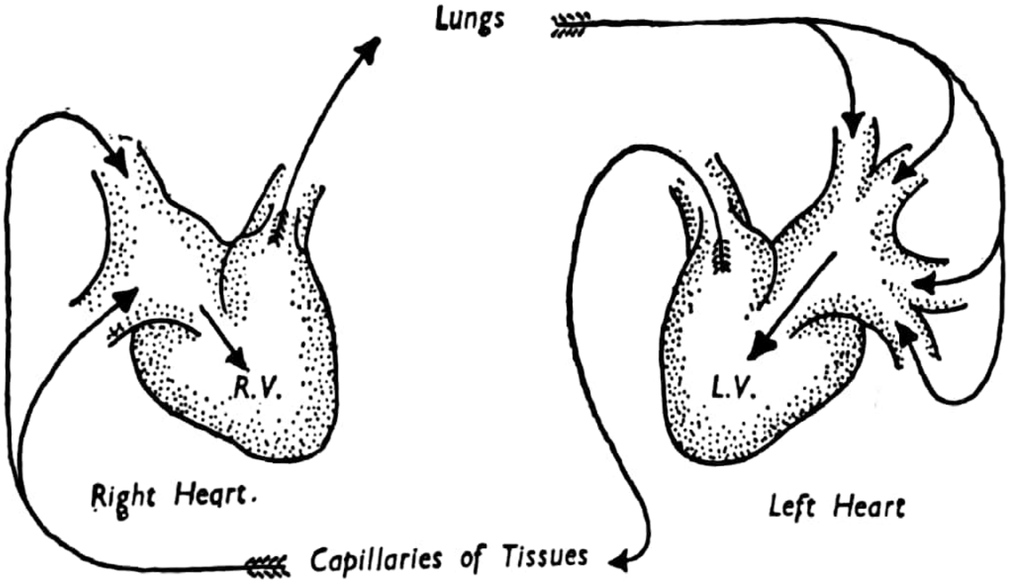


FIG. 19(*a*).—The two sides of the heart represented as separate organs.

In heart disease, which affects the efficiency of the shutting of the valves, these sounds are correspondingly altered ; and though each sound is made up by the closure of a *pair* of valves, one on each side of the heart, by listening at different points over the organ it is usually possible to specify which one is out of order.

It is important to realize that, although the two halves of the heart are welded together as a single organ, they are really performing quite separate mechanical functions. The auricle and ventricle on each side constitute a pair of chambers concerned with the pumping of blood through a particular territory; and though the blood traverses each pump in turn it is quite possible to imagine the right and left halves as two separate organs fixed together for convenience like the crossed vinegar bottles in an old-fashioned cruet (Fig. 19(*a*)). The output of the heart, however, must obviously be the same on both sides; the flow from the left ventricle into the aorta must equal that from the right ventricle into the pulmonary artery or otherwise blood would be dammed up on one or other side. This output, at rest in the adult, is some 6 pints a minute, or in other words the whole of the blood in the body is passed through the heart in something under two minutes.

The Control of the Heart. The heart's activity is varied by a number of factors; these act by altering either the *heart-rate* or its power of contraction, i.e., its *output*. The most important factor influencing output is the inflow of blood from the great veins, for output must be exactly equal to this, whatever changes may occur in the resistance offered by the general circulation, or blood will be dammed up in the venous system; and this is what actually happens in heart failure. The venous inflow in its turn is greatly influenced by the sucking action of respiration. Breathing in produces a negative pressure within the cage of the chest which draws blood into the great veins and right auricle from the venous trunks of the head, abdomen and limbs. And therefore the filling of the heart is largely a rhythmic result of ordinary breathing; a deep breath increases the intake, the output must rise correspondingly, and the pulse can be felt to quicken at the wrist. Conversely, if the pressure within the chest is raised by violent straining exertion, the great veins are flattened out, the cardiac output falls, and the pulse weakens or may even be made to disappear.

From the mechanical viewpoint, the work achieved by the heart, i.e., the energy produced in ventricular contraction, is used up in two ways. The column of blood expelled acquires a definite velocity and therefore a momentum or kinetic energy ; and the elastic resistance of the arterial tree has to be overcome, the stretching of the arterial walls and the resulting tendency to recoil providing a store of potential energy like a compressed spring. In actual fact the greater part of the work done is in overcoming arterial resistance, since the velocity of the blood is unimportant except during violent exercise. It has been stated that, during the course of a normal life, the work done by the heart is equivalent to the lifting of a weight of 10 tons through a height of 10 miles.

The circulatory resistance that has to be overcome is of course exactly equal to the arterial blood-pressure, and the heart adapts itself wonderfully well to expel exactly its intake of blood however the arterial pressure changes ; or, conversely, to get rid of an intake varying between wide limits against a constant resistance. It is comparable to a bath which remains filled to a constant level with the tap running and the outflow pipe open, even though the tap may be turned up or down and the outflow pipe made narrower or wider, or even though both are varying at the same time. The essence of this adaptability lies in the power of heart muscle fibres to contract more forcibly the more they are stretched when an increased intake of blood dilates the organ in the relaxed period of diastole ; and vice versa. This is a phenomenon corresponding closely to Hooke's famous physical law applied to the stretching of elastic non-living matter—*Ut tensio sic vis.*[1] Obviously there are limits to the heart's power of meeting an increased demand by dilating, with increased contraction and hypertrophy of its fibres. One limit is that the fibrous bag or pericardium containing the organ cannot stretch; the other is the increasing mechanical disadvantage at which the stretched fibres have to work. In medical terminology, this property of overcoming handicaps such as a leaking valve or a grossly-raised blood-pressure is known as *compensation*, and it results in the development of an organ which is permanently larger and thicker than normal. But when the limits of adjustment are surpassed cardiac *decompensation* results; output can no longer keep pace with influx, and the veins of the lungs and body become stagnant reservoirs.

The Nervous Control of the Heart. Apart from the self-regulating mechanism just described, there is a nervous control designed to adapt the organ to the needs of the whole organism. And this is effected by branches of the two constituents of the independent autonomic or vegetative nervous system—the sympathetic and parasympathetic. As we have seen in connection with the bowels and bladder, the two have mutually antagonistic actions, but work in collaboration to achieve a balanced control (Fig. 19 (*b*)).

The *parasympathetic* fibres are derived from a nerve called the *vagus*, running down from the base of the brain through the neck and chest. They exert a constant depressing action on the heart, slowing down its rate and weakening its force of contraction. If the nerve is stimulated experimentally, the heart may stop altogether; similarly, firm pressure on the eyeball

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[1] "As is the tension, so is the force."

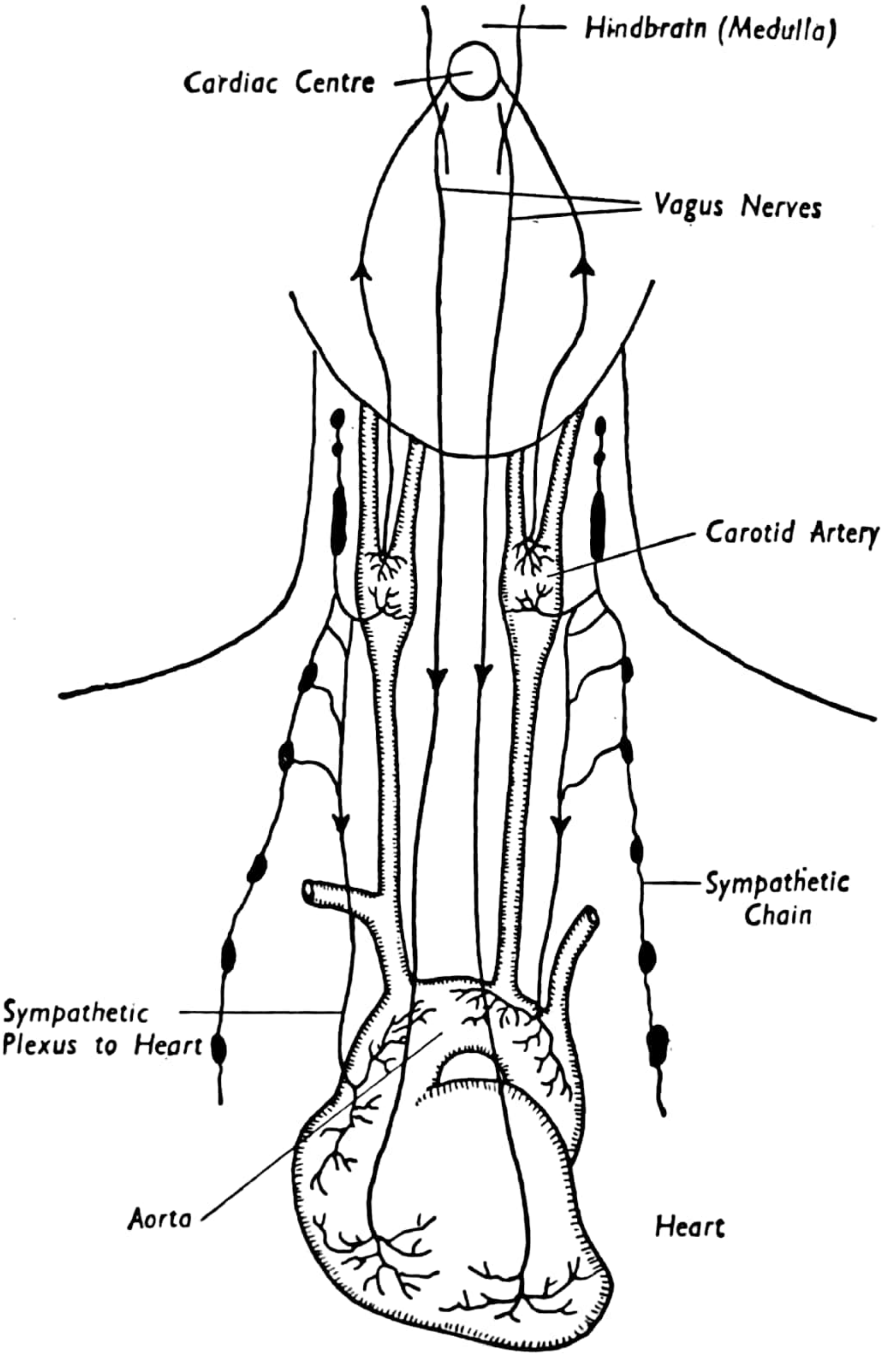

FIG. 19(*b*).—The nervous control of the heart; anatomical arrangements.

(Adapted from Starling's *Principles of Human Physiology.*)

excites the vagus reflexly and slows the pulse. Vagus action is achieved ultimately by the liberation at its nerve-endings in the heart muscle of a particular chemical substance—*acetylcholine.*

The *sympathetic* fibres are derived from the sympathetic chain which runs the length of each side of the spinal column, and their action is to accelerate the heartbeat and increase the force of contraction, which they do by the liberation of *adrenaline* at their terminals. The heart is very sensitive to this substance, which is also, and indeed mainly, produced by the adrenal glands; adrenaline from the adrenals reaches the heart via the

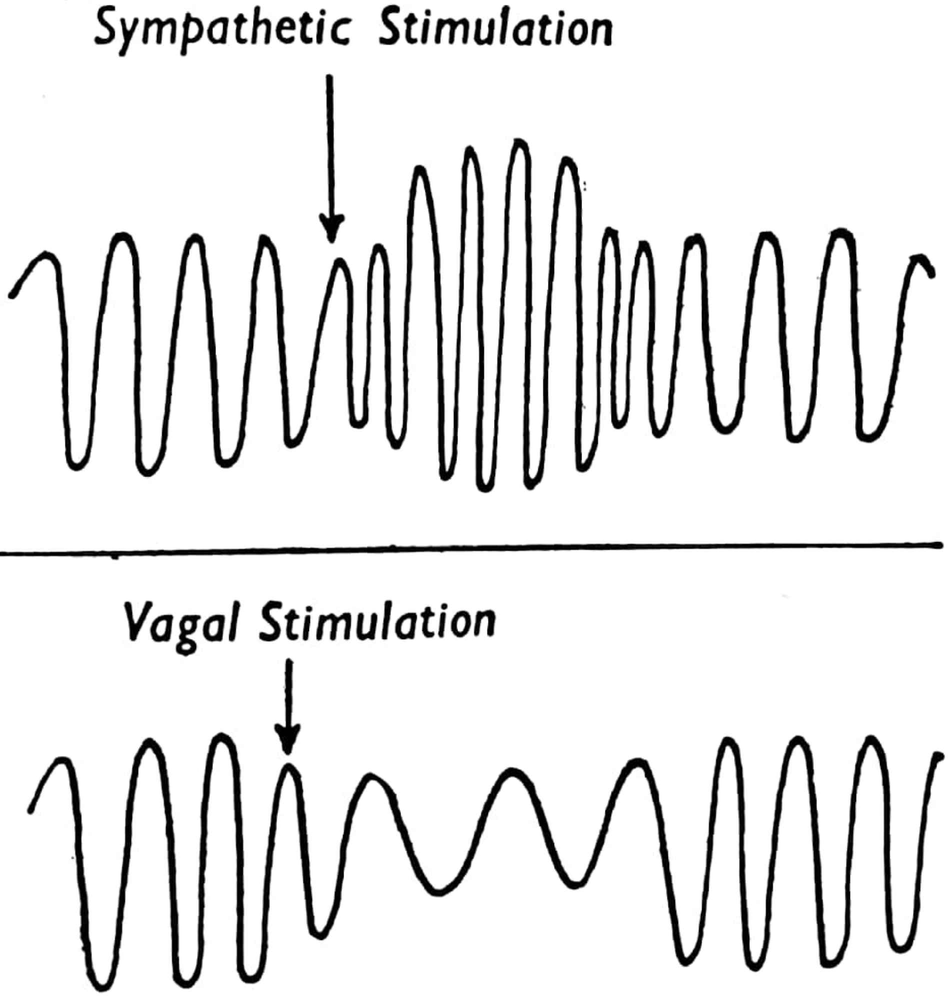

FIG. 20.—The nervous control of the heart.

Sympathetic stimulation produces a rapid forceful beat, parasympathetic action a slower beat of less amplitude.

circulation at times of anxiety and stress, producing a rapid forceful beat.

The ultimate cell-stations from which all these fibres, both sympathetic and parasympathetic, are derived are found in the hind-brain or medulla, where they form two centres, one inhibiting and one accelerating cardiac action. These function as central exchanges which control the heart on the basis of information received from various parts of the body, and in particular from the heart itself and the great arteries—aorta and carotids. These messages indicate the degree of filling of the heart, the blood-pressure, and the extent of cardiac dilatation ; and the controlling centres react so as to secure that the heart accelerates if its venous intake increases or the arterial pressure falls, and slows down if these changes are reversed.

It is necessary finally to say a few words on the metabolism of the heart muscle itself. The heart gets its blood supply from two tiny but all-important vessels, the coronary arteries, which spring from the aorta at its commencement and ramify out over the surface of the organ. These little vessels are very sensitive to nervous control and to changes in oxygenation of the blood, and respond so as to secure the necessary increase of blood-supply to the wall of the heart when extra demands are made on it. Any coronary disease or obstruction by clot (coronary thrombosis) gravely interferes with the capacity of the heart to respond to demand, and in consequence there is a risk of fatal results on exertion. From the biochemical aspect, the great energy output of the heart muscle is obtained partly by utilization of its rich store of glycogen and partly by use of lactic acid circulating in the blood, an activity peculiar to itself and not shared by the ordinary muscles of the body.

The Circulation. We have already mentioned that there is a *pressure gradient* throughout the circulation, falling as we pass from the left side of the heart through the arteries and capillaries until it becomes very low or zero in the veins. This pressure is usually measured in the length of a counterbalancing column of mercury. It is much the same in all the arteries, whether in the aorta or at the wrist, i.e., some 120 mm. of mercury. But it falls to 20 mm. in the capillaries of the tissues, and only a few millimetres when these have rejoined to form the main veins. In fact, in the large veins of the neck and chest the pressure is often negative because of the sucking action of respiration. Arteries when cut across bleed from the end nearer the heart, in forcible spurts derived from the impetus of left ventricular contraction. Veins bleed from the cut end farthest from the heart, in a steady gentle flow. And wounds of the larger veins of the neck often actually suck in air from outside, so low is their internal pressure ; this is a great danger to the circulation, for the air gets churned up into foam in the heart and obstructs the smooth flow of blood.

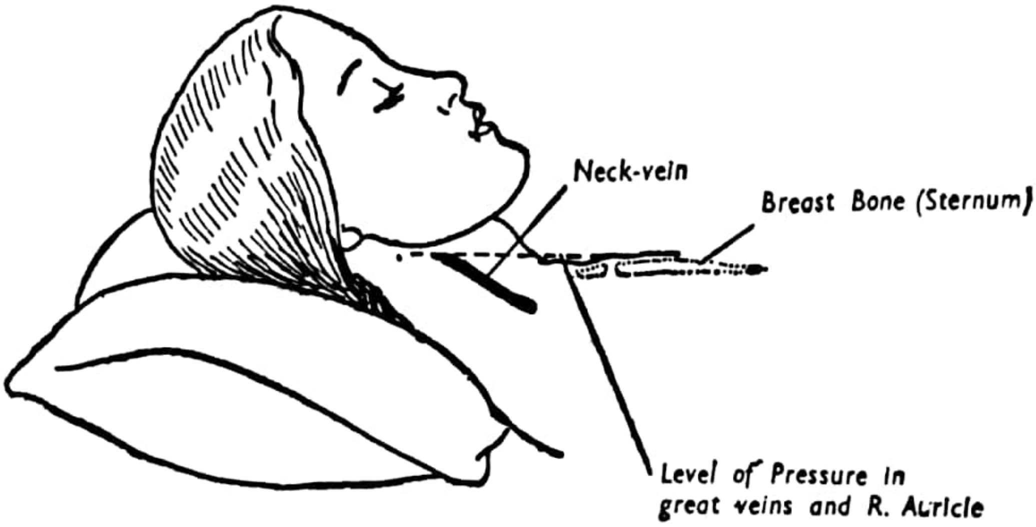

FIG. 21.—The basic level of venous pressure in the reservoir of the right auricle of the heart is shown by the extent of the visible column of blood in the superficial veins of the neck.

It must be realized that the blood-pressure in the arteries is alternately high and low, corresponding to the contraction and relaxation of the left ventricle. The *systolic pressure* in man is some 130 mm. of mercury, the *diastolic pressure* only 70 mm., and the fluctuation between is spoken of as the *pulse pressure*, i.e., 60 mm. In the veins and capillaries on the other hand there is no pulsation and the pressure is a steady one. The term " blood-pressure " in common medical and popular usage always refers to arterial pressure and is expressed in double figures as 130/70, though there is a considerable normal range of variation in different individuals. Since the higher systolic figure depends on the force with which the left ventricle contracts, and since this in turn is greatly influenced by emotion and exertion, it is the relatively steady diastolic pressure which provides a constant base line and gives a clue to any abnormal changes in circulatory disease.

A basic feature of the circulation is that the intermittent flow from the heart into the great arteries is converted into a constant flow by the time the tissue capillaries are reached ; and this is due to the elastic recoil of the arteries and arterioles which continues to provide a driving force while the heart itself is relaxed in diastole.

The time taken for the blood to pass from any given point in the circulation, say an arm vein, through the heart and lungs and back to the same point is known as the *circulation time*, and is of the order of 25 seconds at rest, though speeded up in exercise. It is easily measured by injecting a substance which is identifiable because of its colour or radio-activity and noting the time before its reappearance. It does not, of course, imply that the actual speed of the blood in its passage is constant, as this varies with the heartbeat and the size of the blood vessel ; at its maximum, in the great arteries springing from the heart, the velocity is rather more than a mile an hour. Nor must we confuse the velocity of the blood flow with that of the pulse wave, for this is a pressure wave transmitted through the column of blood contained in the arteries with great rapidity, and is quite unrelated to any forward movement of the fluid itself. It is in fact transmitted at a speed of some 15 miles an hour.

We have seen that the main arteries divide and subdivide into a network of tiny arterioles and capillaries of a total cross-section many times greater than that of the aorta ; it is this capillary bed which provides the main resistance to the thrust of the left ventricle. But it is not a fixed resistance, for the arterioles have muscular coats, and the capillaries, contractile cells in their walls, which are intimately subject to control by nervous and chemical agents. It is as if a hose-pipe divided into innumerable smaller branches which were not only elastic but could be altered in calibre ; we speak of *vasoconstriction* when these are narrowed and *vasodilatation* when they are opened up. This provides a means for adjusting the dynamics of the local circulation in different parts of the body ; such an arrangement is absolutely necessary to meet changes of circumstance, for example the changing effects which gravity exerts in different postures.

In standing upright, the whole of the blood in the body would collect in the small vessels of the abdomen and legs (and could easily be accommodated there) were these not shut down to a considerable extent by a vasoconstriction which prevents such an influx. It is obvious that such a widespread narrowing must be reflected in a general rise of blood-pressure throughout the body, as the remaining vessels are overstretched ; conversely, an extensive vasodilatation leads to stagnation of blood and a fall of blood-pressure. In fact, the enormous vascular area provided by the abdominal organs forms what is known as the *splanchnic pool*, in contrast with the *somatic* part of the capillary bed in the skin, muscles and skeleton. When the splanchnic vessels are widely dilated, as after a heavy meal, the blood-pressure falls and the blood-supply to other parts, particularly to the brain at the highest level, is decreased. We become sleepy and tend to lie down because there is a temporary cerebral anaemia and the circulation can be maintained more easily in the horizontal position. Fainting or *syncope* is an acute change of exactly the same nature after an emotional shock which produces splanchnic vasodilatation. And in what is known as *surgical shock*, which comes on in the hours following severe injury or burns, there may be such widespread expansion of the capillaries that the body " bleeds to death into its own blood vessels ", the blood-pressure falling profoundly and too little blood being available for the heart to work on or the lungs to aërate. Thus, in some ways, the circulation is to be compared, not to a main railway line, but to a whole railway system with numerous sidings but only a constant number of trains. If some of these are shunted off into the sidings to remain idle the main line traffic will be much less heavy, i.e., the blood-pressure will fall. If all the trains are in use and the sidings empty, the traffic is intense, i.e., the blood-pressure rises. Such a regulation occurs in all parts of the body ; any inflammation in the skin or elsewhere sets up a local vasodilatation which flushes the part with blood. And in these circumstances the arterioles may be so widely opened that they communicate their pulse to the normally pulseless capillaries and the whole part throbs.

The mechanism controlling the small vessels of the body corresponds to that of the heart and is a double one—partly nervous, partly chemical. The sympathetic fibres which accelerate the heart also constrict the vessels, and are thus fundamentally concerned with preparing the body for emergency and violent action ; for they divert the blood from the skin and non-essential organs to the muscles, and to the blood vessels of the brain.

The parasympathetic fibres promote general relaxation and fall of blood-pressure ; but the two systems are collaborators and the vessels are never completely shut down, and never completely dilated (except in severe shock), but possess a normal *tone* which varies between wide limits.

On the chemical side, the arterioles and capillaries are very sensitive to circulating adrenaline, which has the same effect as the sympathetic nerves ; and are dilated by certain substances liberated from the tissues when they are bruised and injured, e.g., the substance *histamine* which is thought to be partially responsible for the phenomenon of shock after wounding. And again, as in the case of the heart, the ultimate controlling (vasoconstrictor and vasodilator) centres are situated in the medulla. To a certain extent it is true to say that the prime function of these centres is to ensure that, whatever else happens, the supply of blood to the brain itself is safeguarded ; for other tissues can survive deprivation of oxygen for many minutes, perhaps an hour or more, but the brain cells must die after more than a few minutes of anoxaemia.

A beautiful example of this mechanism is seen after blows or falls on the head severe enough to cause progressive bleeding within the rigid and unyielding bony skull ; such bleeding steadily compresses the brain and makes it more difficult for blood to be pumped into it from the heart. The vasoconstrictor centre in the medulla reacts to this by so shutting down the vessels all over the body that the general blood-pressure rises, increasing to enormous heights; this enables blood to be forced into the brain-box, at any rate until the whole process of adjustment breaks down.

Exercise. There is one particular point in connection with the regulation of the circulation which, though found in animals, is most developed in man. Although the heart and vessels are quite capable in themselves of adjusting to meet the needs of a particular situation, they are anticipated by mental factors which produce the same changes before they are strictly necessary. Thus the emotion implicit in waiting to start running a race produces a rise in blood-pressure and pulse rate long before these are made physically necessary by the demands of active muscular contraction.

When strenuous exercise is actually in progress, the oxygen demands of the muscles may be ten times those of the resting stage; and this must be met by a corresponding multiplication of cardiac output. This is because arterial blood is already saturated with oxygen and cannot dissolve more; the only way to bring more oxygen to the tissues is to rush the blood round the circulation at a faster rate, loading oxygen in the lungs and unloading it in the tissues more times in a minute. This is obviously comparable to increasing the food supply to this country during a period of emergency by a quicker turn-round at the ports on each side; there is faster loading and unloading at the docks though the number of ships available remains the same.

But the bodily changes in exertion are very complex. Muscular contraction speeds the return of blood to the heart by milking it upwards in the veins of the limbs;

and this increase in venous inflow must, as we have seen, imply an equivalent increase in cardiac output if the heart is not to fail. The total amount of blood in the circulation cannot be increased, but more can be diverted to the muscles by shutting down the vessels of the skin and the splanchnic area, and by the contraction of the spleen, an organ which can squeeze out quite a large amount of blood into the general circulation when necessary. The exaggerated respiratory movements suck more blood into the great veins of the chest as well as more air into the lungs. The increased activity of the sympathetic system, aided by the pouring out of adrenaline into the blood which accompanies any excited state, increases the heart rate and the force of each beat, and mobilizes the liver glycogen as sugar to be used by the muscles. And the waste products of muscular contraction—carbon dioxide and lactic acid —stimulate the brain centres controlling the heart, the vessels, and the rapidity and depth of respiration, to continue the effects which emotion has initiated.

The Lymphatic System and the Lymph. The lymphatic system is a sort of accessory to the main vascular system. Not all the fluid portion of the blood which exudes into the tissues from the capillaries returns to these vessels. As a result tissue fluids accumulate, and the excess is removed by a separate set of fine channels, the *lymphatics*; these begin as clefts and crevices between the cells and join up to form a plexus of lymphatic vessels draining the various organs. They pass up the limbs and trunk, and are interrupted at certain points by a number of *glands*, filter or stations which lie in the limbs at the elbow and knee, armpit and groin, and in the trunk alongside the great vessels like the aorta. The lymphatics of the trunk join a wider vessel known as the *thoracic duct*, of matchstick calibre,

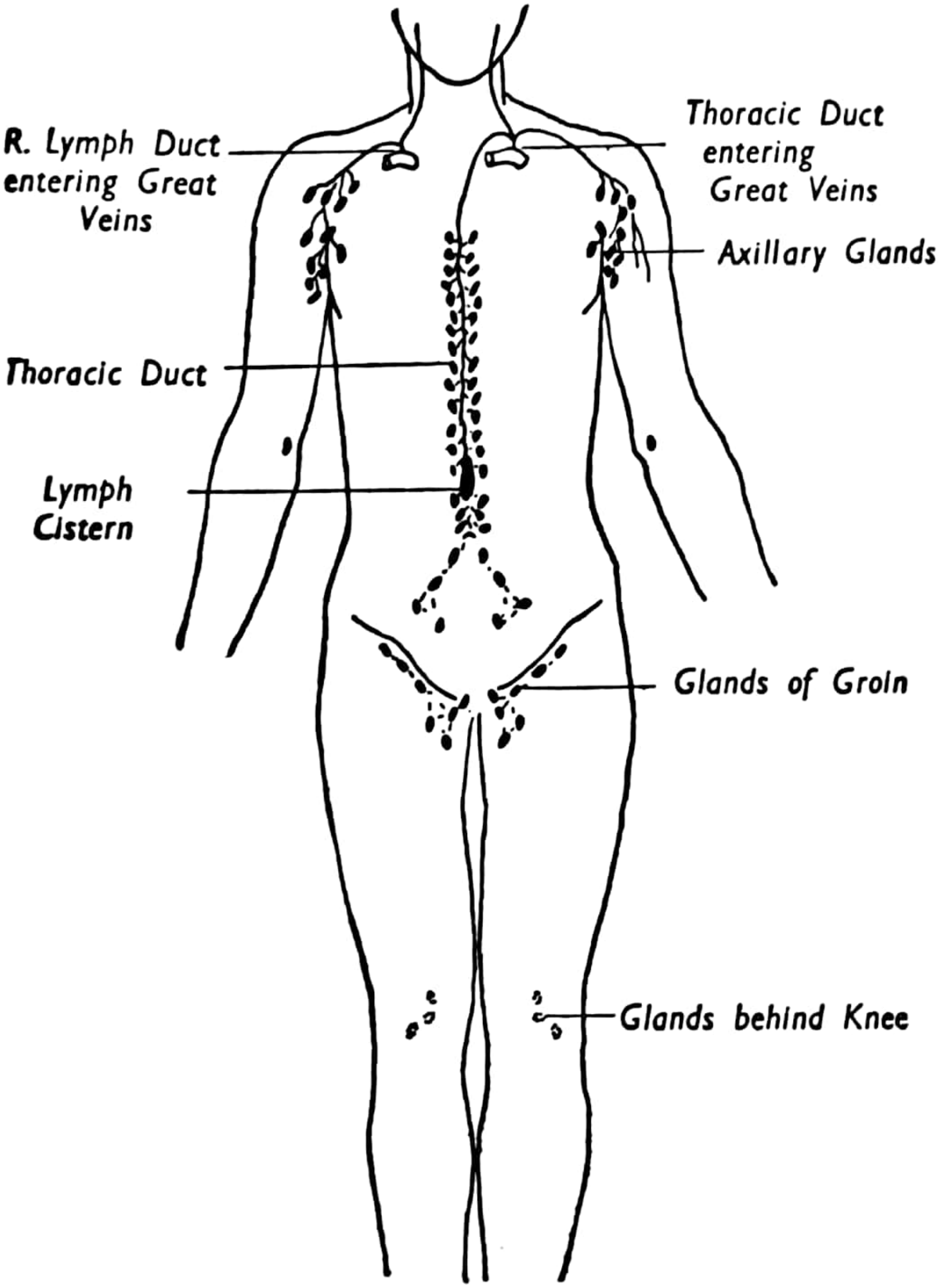

FIG. 22.—The lymphatic system. (The glands of the head and neck are not shown.)

which runs up in the chest to the left side of the neck; there it gathers the lymph vessels of the left arm and left side of head and neck, and discharges into the great veins. The vessels of the right arm and right side of head and neck behave similarly, only they have no thoracic duct to join. One of the main functions of the lymphatic system is the absorption of digested fat from the lymphatics or lacteals of the bowel, while the glands deal with any infection brought to them by the lymph vessels.

It has been pointed out that the blood nowhere comes into contact with the tissues, the walls of the capillaries intervening. The actual nutrition of the cells has to be achieved by the tissue fluid, which permeates the clefts and spaces and passes on dissolved nutriment derived from the blood. There is in fact a continuous oozing out of the fluid element of the blood from the capillaries to become tissue fluid; and this implies the necessity of an equivalent means of draining away the excess of fluid. This is what is provided by the lymphatic vessels. The actual threadlike vessels run longitudinally up the limbs and trunk in company with the main arteries and veins. There is little or no positive pressure in the lymphatic system, but the vessels are valved like the veins, so that the impulses transmitted by the beating of adjacent arteries and the contraction of surrounding muscles results in an inevitable upward flow. The lymph itself is a pale yellow fluid which clots on standing like blood and contains a number of lymphocytes similar to those of the blood. We have already seen that the lymphatic system of the intestine plays the main part in the absorption of fat, so that lymph obtained from the thoracic duct after a meal is milky and opalescent with fat globules.

The main function of the lymphatic system, apart from drainage of excess tissue fluid and fat absorption, is the cleansing from the tissues of particles of foreign material, particularly in dealing with infection. Small crystalloid molecules are absorbed directly into the blood-stream, but larger colloid particles and suspensions of solid matter, like the ink used in tattooing and the dead bodies of micro-organisms, are slowly conveyed up the lymphatics to the nearest gland station. This usually deals effectively with bacteria and their toxins, as each gland is an intricate filter of winding channels, packed with white blood cells which deal with the invasion. Occasionally however the mechanism fails, the lymphatic vessels and glands themselves become acutely inflamed, and the infection has to be dealt with by the next gland station or may even enter the blood-stream and cause a general *septicaemia*, or blood-poisoning.

Inflammation and Infection. This is a convenient point to discuss the phenomena of inflammation and the defences of the body against infection generally. The human body is liable to attack from three sources : (i) *viruses*, like those of infantile paralysis and chicken-pox, which are so small as to be invisible under the microscope and can traverse even very fine filters ; (ii) *bacteria*, visible microscopic organisms like those of plague and typhoid ; and (iii) larger parasites which are single cells but still of microscopic size, the *protozoa* of malaria, syphilis and other diseases.

The primary defence against these is of course by the outer coverings and internal linings of the body, the normally intact " epithelial envelope " mentioned on p. 17. The horny layer of the skin is a physical obstacle. The mucous membranes are more sensitive, but even here organisms are entangled in sticky mucus or wafted away by the waving hair-like processes of the cells in certain regions (e.g., the lining of the wind-pipe), or the secretion of the glands may itself be actively bactericidal, like the tears. We may say that an intact lining is normally proof against invasion except in certain sites and with certain organisms, notably the gonococcus which causes gonorrhoea and can apparently traverse the healthy mucous membrane of the urethra.

Once organisms have gained access to the tissues, however, the essence of the defence lies in their being killed and swallowed-up by special cells which can wander to the affected part. These cells are known as *phagocytes* and the devouring process as *phagocytosis* ; this process applies as much to the débris of destruction and repair as to the organisms themselves. To a certain extent, in the most minor of injuries and infections, the process can be completed by the phagocytes available in the part, without any changes in the local circulation. But usually it is necessary to bring up reinforcements by increasing the available blood-supply of the region to provide a much greater number of phagocytes from the granulocyte white cells of the blood. All the capillaries dilate widely and are occupied by a hurrying central stream of red cells, with white cells clinging to the margins. The granulocytes can move about independently and now make their way through the capillary wall to the site of infection, where they accumulate in crowds. As soon as the infection has been overcome, and the débris removed, the injured tissue is repaired by an overgrowth of fibrous tissue in the depths of the wound and an ingrowth of surface epithelium to cover any superficial breach.

Though the reactions to injury and infection are essentially similar, the latter is characterized by the much greater number of phagocytes necessary. In an infective focus which is still unresolved after 48 hours *pus* begins to form at the centre, the pus being a fluid collection of dead phagocytes and bacteria. On the other hand pus formation is entirely absent in wound healing unless a secondary infection develops.

Inflammation is marked by warmth and redness of the part—due to its increased vascularity—by swelling—due to the exudate of tissue fluid from the capillaries—and by pain—due to stretching of nerve endings—the four classical signs of *rubor*, *calor*, *turgor* and *dolor*.[1]

The reason for the migration of leucocytes from the blood is that they are attracted towards chemical substances produced by the bacteria, or for that matter by the presence of any foreign protein, an attraction spoken of as *chemiotaxis*. And this is facilitated by a substance found in damaged tissues which increases the permeability of the capillaries. Only when an infection becomes stubborn and chronic, as in foci of tuberculosis, do the lymphocytes of the blood come to play a prominent part in circumscribing the lesion.

So far the phenomena we have described are the physical ones visible to the naked eye, or with the microscope, and confined to the affected part. But superimposed on these, invisible, and operating throughout the body even while the infection remains a local one, is a whole series of chemical mechanisms of defence, a defence in depth as it were. This defence is made necessary by the fact that bacteria, in addition to the local damage they cause, may affect the body as a whole. This they do either by invasion and spread through the blood- and lymph-streams with widespread multiplication in the tissues ; or by forming a poisonous toxin which circulates in the blood ; or both. These toxins, e.g., those of diphtheria or tetanus, are of extreme virulence and may cause death while the bacteria themselves remain localized to a small site in the throat or a wound. Moreover, they have specific actions on certain body systems only, such as the brain or the red blood cells.

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[1] Redness, heat, swelling and pain.

Different species of animals show great variation in their susceptibility to toxins, and some are quite unaffected by certain diseases, e.g., the dog by typhoid; they possess a *natural immunity*. As is well-known, after recovery from most of the infectious fevers, man develops a permanent resistance to second attacks; this is spoken of as an *acquired immunity*. And since he owes this to having suffered an attack of the disease and having overcome it by manufacturing the specific protective substances in his own tissues, it is also described as an acquired *active* immunity. Such an active immunization can also be achieved by giving small doses of toxin or dead bacteria in an inoculation or injection; essentially this acts by producing a minor and very much modified form of the disease, but the active response of the body is as great as with a real attack and guards against any such infection subsequently.

Now it is possible to produce artificially an actively acquired immunity against, say, tetanus, by injecting into a horse first minute and then increasing doses of the toxin, until eventually the animal is able to remain unaffected by enormous doses which would have previously been rapidly fatal. Its blood serum now contains a large amount of antitoxin, capable of neutralizing and destroying the tetanus toxin; and the injection of such serum into a man confers on him what is known as an acquired *passive* immunity—*passive*, since his own tissues have played no part in elaborating the protective agent. But this is of course only temporary, unlike the relative permanence of active immunization, and soon passes off. So it is only of value in the treatment of the established disease, or in trying to forestall it by giving antitoxin as soon as possible after a wound which may have been contaminated with tetanus organisms ; but it is of no value whatever for long-term protection.

It is of interest to note here that babies possess a *congenital immunity* against such infections as measles ; this is essentially passive, since they have derived the protective agents while in the womb from the blood-stream of the mother, who has a permanent active immunity of her own dating from an attack in her childhood. Because the newborn infant's resistance is only passive and borrowed, it lasts a mere six months, and the child is then susceptible.

The protective agents mentioned above are known as *antibodies.* They are formed in the spleen, liver, bone marrow and lymph glands, and they may be antitoxins, which neutralize bacterial toxins ; or antibacterial agents, which clump bacteria together into agglutinated masses and then dissolve them. It will be seen that this mechanism is just another example of the general tendency of the tissues to react against the introduction of foreign protein ; it is, for instance, comparable to the agglutination and destruction of foreign red blood cells which we have previously discussed. Occasionally this essentially protective reaction occurs with such violence as to endanger life, typically in the phenomenon known as *anaphylaxis.* This happens when the interval between the first and second dose of the sensitizing agent is rather a long one ; then the neutralization reaction occurs, not in the blood-stream, but in the tissues, and severe shock and collapse or even death may ensue. Though easy to produce in animals, this is rare in man ; this has not prevented it from being employed as the ingenious basis of detective stories.

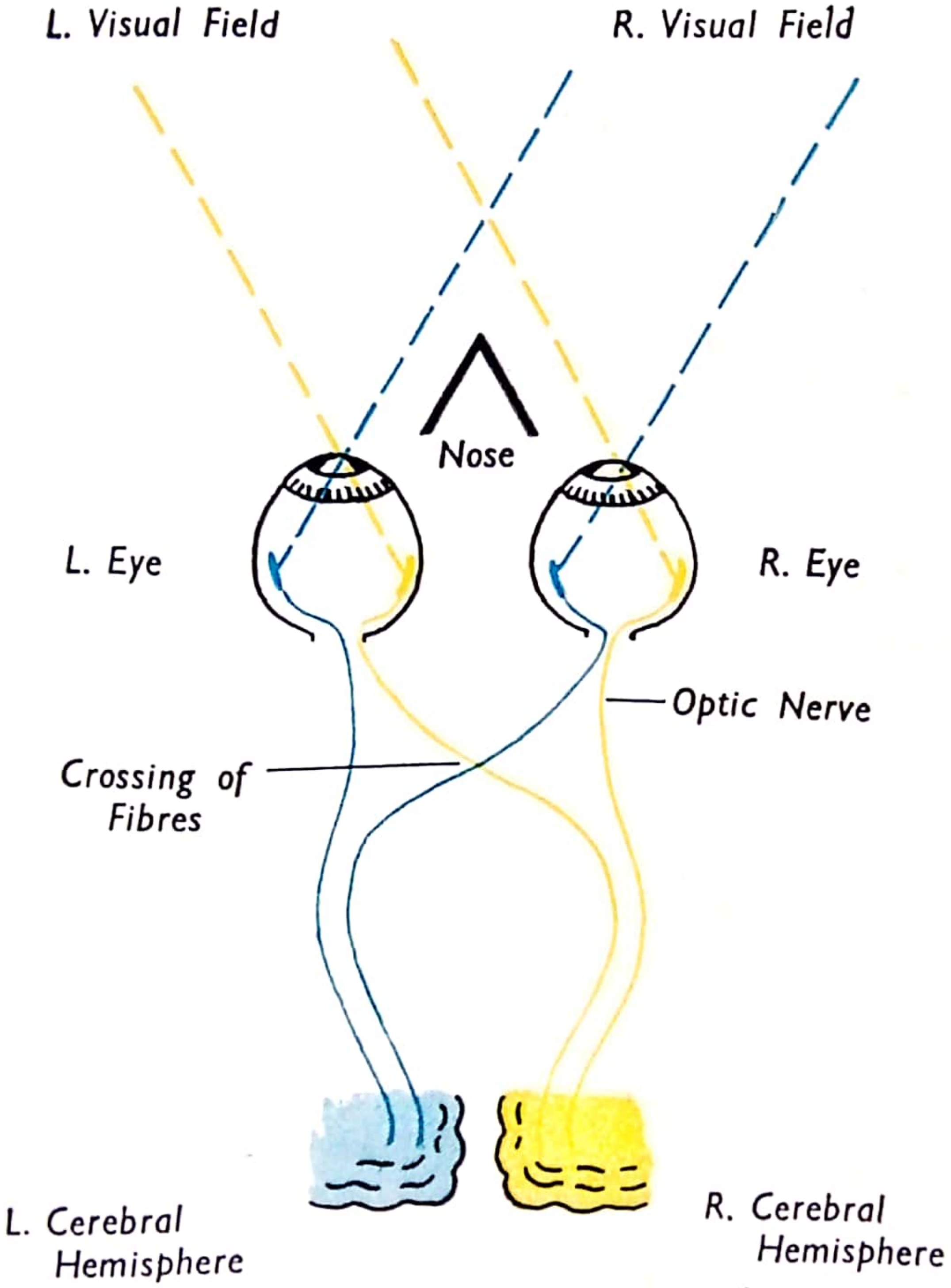

Diagram to show the sorting out of the nerve pathways from the retina which secures that the visual centre in one cerebral hemisphere receives all the impulses arising from the opposite field of vision.

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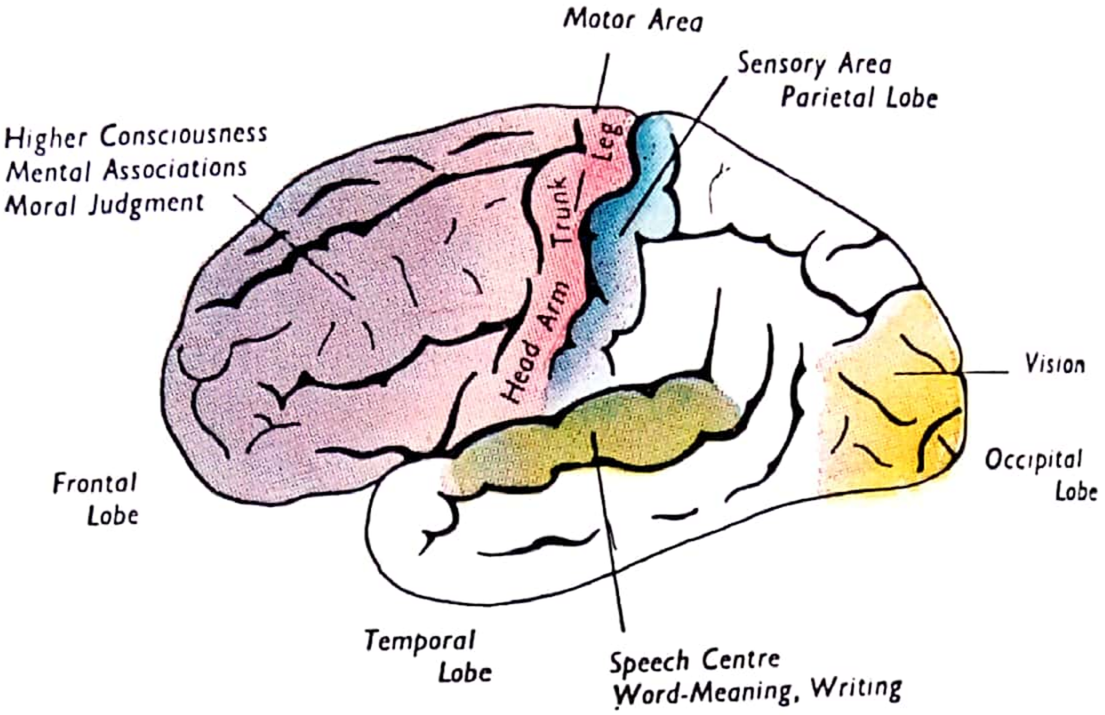
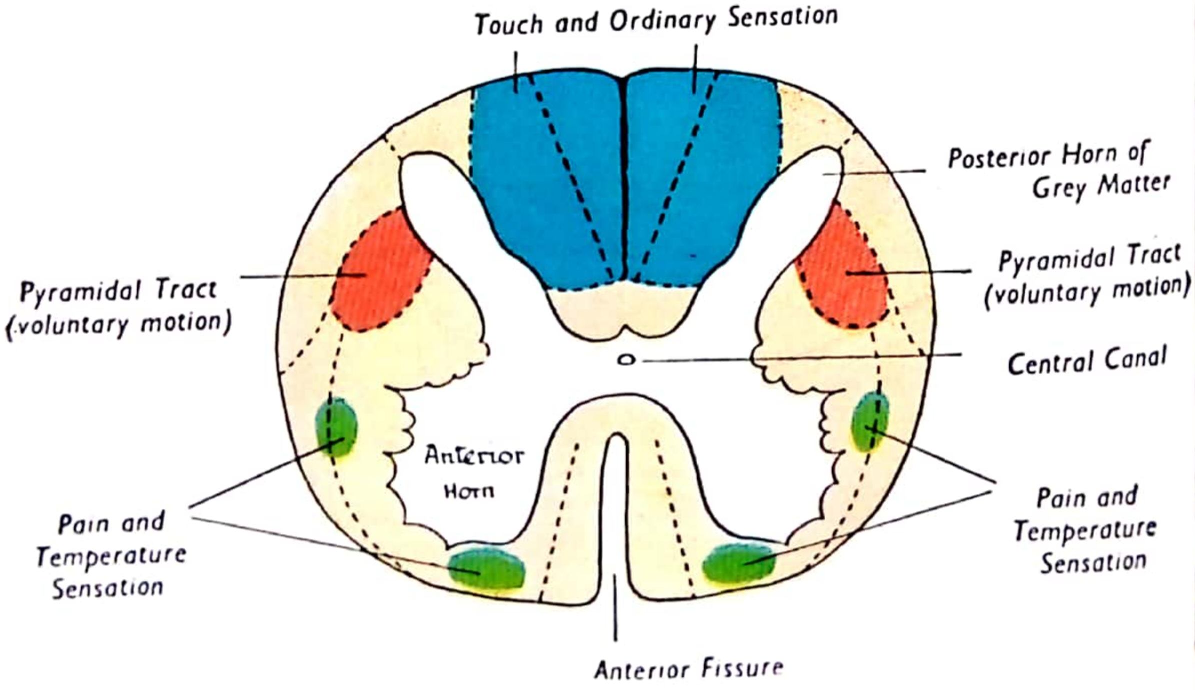


Functional areas in the left cerebral hemisphere. The right side is identical, save for the absence of a Speech Centre.


Touch and Ordinary Sensation
Posterior Horn of Grey Matter
Pyramidal Tract (voluntary motion)
Pyramidal Tract (voluntary motion)
Central Canal
Anterior Horn
Pain and Temperature Sensation
Pain and Temperature Sensation
Anterior Fissure

Cross-section of Spinal Cord, showing the important nerve tracts.

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CHAPTER X

RESPIRATION

The Structure of the Respiratory System. Air inhaled through the nose or mouth enters the pharynx behind them, and then travels down through the air passage proper. The first part of this is the *larynx*, which is also the organ of voice; and this leads on to the wind-pipe (*trachea*) which divides in the upper part of the chest into a right and left *bronchus* for the right and left lung. Each bronchus subdivides within the lung to form numerous branching *bronchioles* which end in clusters of tiny *air-sacs*; and it is in the walls of the latter that the actual interchange occurs between the gases dissolved in the blood and those of the inhaled air.

The cavity of the chest is divided into right and left halves by a massive partition in which the heart lies embedded; the two halves are quite separate and contain the right and left lungs. Each lung cavity is lined by a smooth glistening membrane, the *pleura*, which facilitates the gliding of the lung on the chest wall; and each pleural space is a closed sac, for the membrane is reflected from the deep aspect of the chest wall on to the lung root, and covers the surface of that organ. Normally, there is really no actual pleural cavity, for the two layers of pleura are everywhere in contact, each lung entirely filling its side of the chest. But the lung is a very elastic structure, constantly tending to shrink down and expel its contained air; since in health it cannot do this, there is always a negative pressure in the potential pleural space. The moment that air is admitted to the latter, whether by wound from without or by perforation of the lung from within, the lung immediately collapses into a small solid airless mass. This is made use of in the treatment of pulmonary tuberculosis, where a diseased lung is rested by deliberately letting in air from the outside, a process known as "artificial pneumothorax" treatment.

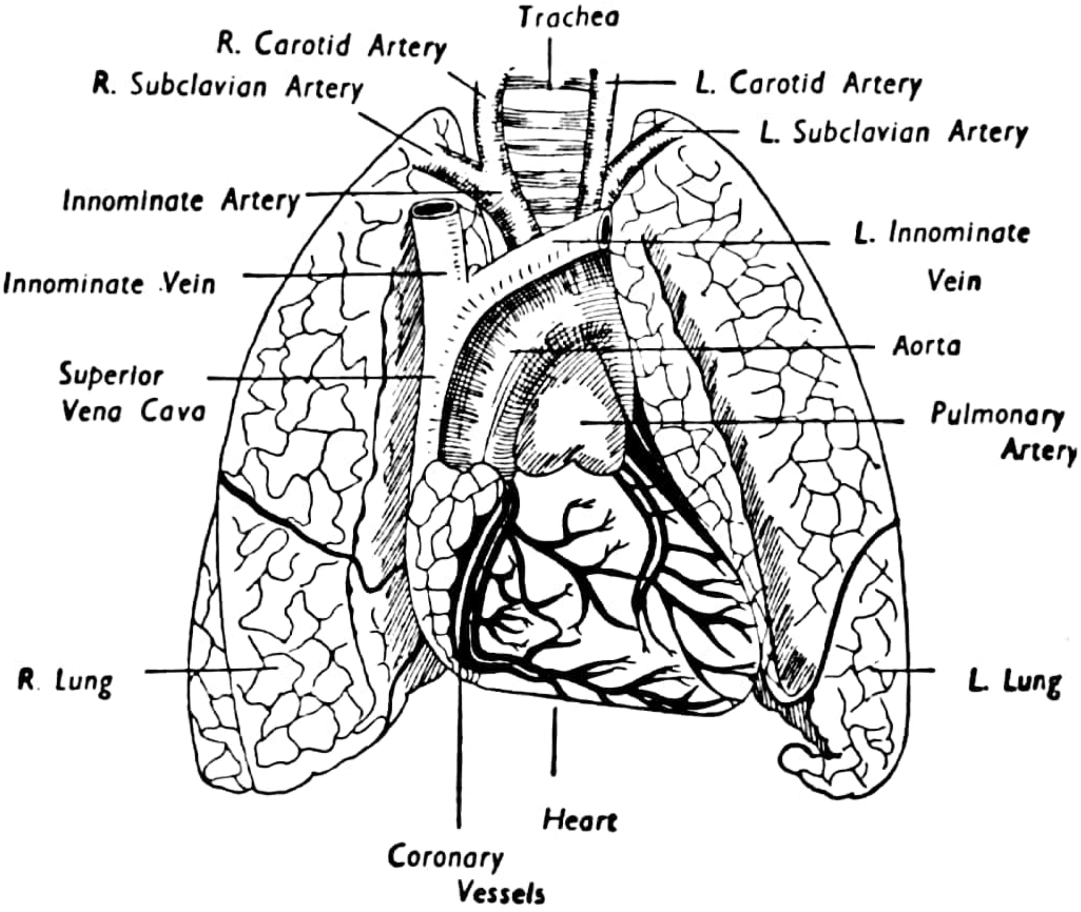

FIG. 23.—Lungs, heart and great vessels, seen from in front after removal from the chest. The lungs normally overlap the greater part of the heart and have been retracted to expose that organ (*Gray*).

Respiration. The purpose of respiration is the entry and exit of air to and from the lungs. In *inspiration* the chest cavity is enlarged and air enters; in *expiration* the reverse occurs. Respiratory movements may be thoracic, or abdominal, or both. In thoracic inspiration the breast-bone is lifted up and forward, and the ribs are simultaneously elevated and come to lie more horizontally ; and the chest is thus increased in diameter both from side to side and from front to back. In abdominal inspiration the diaphragm contracts and flattens down on the abdominal organs, bulging out the abdominal wall and increasing the vertical height of the chest. Thus inspiration is an active process, due to muscular exertion. Expiration, however, is passive ; the chest wall subsides, the abdominal muscles recoil, and the diaphragm relaxes, and air is driven out of the lungs.

Lung Ventilation. During normal quiet breathing about 600 c.c. (40 cu. in.) of air are taken in and breathed out at each respiration, and this steady flow is known as the *tidal air.* By means of a very deep inspiration some 2000 c.c. (135 cu. in.) more can be taken in, the *complemental air* ; and, in the other hand, after a normal expiration it is possible by breathing out very forcibly to expel a further 1200 c.c. (80 cu. in.), the *supplemental air.* The sum of these figures, which is the total possible flow in one direction, is known as the *vital capacity* of the individual and represents the maximum volume of air that can be expelled after as deep an inspiration as possible, i.e.,

Complemental air = 2000 c.c. (135 cu. in.)
Tidal air = 600 c.c. (40 cu. in.)
Supplemental air = 1200 c.c. (80 cu. in.)
Vital capacity = 3800 c.c. (255 cu. in.)

The vital capacity obviously varies a good deal from one individual to another, depending on such factors as physical build and state of fitness and training ; it is also greatest when standing and least when lying down, and is obviously diminished when the ribs and chest are fixed by arthritic disease, a state of affairs predisposing to lung infections. But no expiration, however forcible, can empty the lungs of air ; an irreducible minimum is left occupying the bronchi and air-sacs, the *residual air*, a volume of some 1500 c.c. (100 cu. in.). Finally, in normal breathing it is obvious that not all of the 600 c.c. of tidal air will reach the air-sacs, for some is needed to fill the air passages themselves, a *dead space* of some 150 c.c. (10 cu. in.).

We must not allow ourselves to be led into regarding these air passages as rigid tubes of standard cross-section. In fact, they have a strong muscular coat in their walls which is capable of considerable alteration of their calibre by constriction or relaxation, so altering the volume of the dead space and the resistance to the flow of air. Asthma is an intense spasm of the bronchial muscle and makes the expiratory act a long-drawn-out effort ; inspiration is less hindered, for it is produced by active contraction of the rib-muscles and diaphragm, whereas expiration is merely a passive relaxation without the impetus to overcome the bronchial spasm. Like the smooth muscle of the blood vessels, that of the bronchi is under the control of the parasympathetic and sympathetic nerves ; it is the latter, in exertion and fright, which open the air-passages widely so as to achieve the maximum possible influx of air to the lungs. Consequently, adrenaline, which stimulates the sympathetic nerve endings, may be injected to overcome an attack of asthma.

Chemical Aspects of Respiration. In the tissues of the average man some 400 c.c. (27 cu. in.) of oxygen is used every minute to burn up food material, and this results in the production of a considerable quantity of carbon dioxide. The oxygen is taken by the tissues from the blood in the capillaries and the carbon dioxide returned in exchange, so that the venous blood leaving any part contains less oxygen and more carbon dioxide than the arterial blood which entered it. The lungs exist to reverse this state of affairs in the venous blood, restoring its oxygen quota and expelling its excess carbon dioxide by gaseous interchange with the air in the air-sacs. Thus the venous blood is rendered arterial in its passage through the lung capillaries; and thus the changes in the tissues are ultimately reflected in changes in the composition of the tidal air which, when breathed out, contains less oxygen and more carbon dioxide than on inspiration. This is made clear by analysis of the composition of inspired and expired air:

	Oxygen	*Carbon dioxide*	*Nitrogen*
Inspired air . . .	20·95%	·05%	79%
Expired air . . .	16·5%	4·0%	79·5%

The content of nitrogen, a gas inert from the respiratory point of view, is unaltered in fact, but appears to be in slightly greater concentration in the expired air, for the reason that slightly less air is breathed out than is breathed in. And the reason for this is that the volume of carbon dioxide exhaled is slightly less than that of the oxygen for which it is exchanged. This ratio:

$$\frac{\text{carbon dioxide output}}{\text{oxygen consumption}}$$

is always less than unity and usually about 0·85. As we have seen in Chapter V, p. 45, this ratio or *respiratory quotient* depends on the exact nature of the foodstuffs being burnt at the time in the body.

The respiratory gases are carried between the lungs and the tissues dissolved in the blood, and measurement shows that the total gas which can be expelled from a given amount of blood is some 70 volumes per cent. Of this, the relatively insoluble nitrogen forms only a small proportion. And, as we should expect, analysis of venous and arterial blood reveals their different gaseous content :

	Oxygen	*Carbon dioxide*	*Nitrogen*
Arterial blood . .	19	50	1
Venous blood . .	10·5	58	1

expressed in volumes per cent.

But the problem is not a simple one of relative solubilities of oxygen and carbon dioxide, for it is affected by the following factors :

(i) The amount that can be dissolved is proportional to the pressure of the particular gas in the surrounding medium, i.e., in the lungs or tissues.

(ii) The gases are not held in simple solution but in loose chemical combination, the oxygen with the haemoglobin of the red blood corpuscles, the carbon dioxide with the carbonic acid and sodium bicarbonate of the plasma.

(iii) The two gases, oxygen and carbon dioxide, can be regarded as opponents which tend to displace each other from their combinations with corpuscles or plasma.

Taking each in turn the processes at work are as follows :

Oxygen. When venous blood, with its reduced content of oxygen at low pressure, reaches the lungs, it is exposed to a higher pressure of oxygen in the alveolar air contained in the air-sacs. The pressure gradient is towards the blood, and oxygen is taken up by combining loosely with the haemoglobin of the red cells to form oxyhaemoglobin. When the blood has been swept through the left side of the heart and round to the capillaries in the tissues, it has arrived at a region where oxygen has been used up in combustion and is at a lower pressure than in the blood ; the gradient sets the other way, and oxygen is set free from the oxyhaemoglobin and diffuses out into the tissue fluid. But, at the same time, this dissociation of oxyhaemoglobin is accelerated or catalysed by the presence in the tissues of the excess carbon dioxide formed by combustion. In other words, the very waste products which have been formed with the using-up of oxygen act as stimulants to the liberation of oxygen from its bound state in the blood so as to make more available to the tissues.

Carbon Dioxide. The pressure of this gas is high in the tissues where it accumulates as a waste product, much higher than in the fresh blood brought to the part by the arteries. The pressure gradient therefore favours the passage of the gas from the tissue fluid into the capillaries, where it enters into loose combination as carbonic acid and sodium bicarbonate in the plasma. This is carried with the venous blood through the right heart and round to the capillaries of the lungs, where it is exposed to the freshly inhaled air in the alveoli ; this air has a very low carbon dioxide content, the gradient sets the other way from the blood, and the gas is expelled with the exhaled air. At the same time, this transference is assisted by the simultaneous saturation with oxygen which is occurring in the lungs, as a high oxygen content in blood tends to break up the loose carbonic compounds.

Tissue Respiration. What we have so far been describing is sometimes referred to as " external respiration ", as it is concerned only with gaseous interchange in the lungs and tissue capillaries, and not at all with the vital processes in the tissue cells themselves. This latter and less obvious process is called " internal respiration ", and is the source and motive of all the obvious and complex apparatus of heart, lungs and circulating blood. Every tissue uses up oxygen and liberates carbon dioxide to obtain its energy requirements, and the amounts involved depend on the state of its functional activity ; obviously they are greatest in the intensively active tissues of the heart, brain, liver and contracting muscles. The process can be studied experimentally by removing thin slices of living organs or making ground-up cellular suspensions, and keeping them in a warmed fluid medium containing dissolved food and oxygen. In actual fact, we know little about the fundamental processes in the living cell which intervene between the intake of oxygen and the ultimate formation of carbon dioxide. There is a complex system of enzymes and catalysts at work, known generally as *oxidases* and these are very susceptible to modification by toxic substances. Thus, the poisonous action of the cyanides is due to their widespread inhibition of tissue respiration. Finally, it should be stated that this method of respiration, involving the use of oxygen, is known as *aërobic*. Many bacteria and other organisms are capable of an indirect respiration without using oxygen, though still forming carbon dioxide, an *anaërobic* process ; but this, though possible to a certain extent in human tissues, is not of any great practical importance.

The Regulation of Respiration. The respiratory act is a complex one, involving the muscles of the nostrils, the larynx, chest wall, diaphragm, and abdomen, so that accurate co-ordination at a higher level is necessary. This control is achieved by a *respiratory centre* of nerve cells situated in the medulla or hind-brain ; it is one of the group of vital centres in this region, which includes the cardiac and vasomotor centres. And it consists of two parts, one controlling inspiration, one expiration. It is obviously important that the centre should be subject to constant influence by nervous information from the lungs and other parts ; and that it should be sensitive to changes in the oxygen and carbon dioxide content of the blood circulating through the cerebral vessels, so that it may react to alter the character of respiration as needed. It is essentially automatic and unconscious, though we are capable of controlling our breathing at will at any time by a superadded voluntary effort. And it is one of the most fundamental activities; in progressively deep anaesthesia or poisoning, respiration is one of the last bodily functions to stop, though it usually ceases before the heart makes its last beat.

1 The *chemical control* of respiration is effected by the response of the centre to changes in the oxygen and carbon dioxide content of the blood; of these two the carbon dioxide is more important, for it is of prime importance to get rid of any excess of waste products, whereas the oxygen content of the air is amply sufficient for respiration within wide limits of variation. The slightest rise of carbon dioxide increases the rate and depth of respiration, and an increase of the content of the gas in the air to only 1·5 per cent multiplies the lung ventilation by half. In progressive asphyxia, with accumulation of carbon dioxide, respiratory convulsions develop followed by collapse and death. On the other hand, there is much less sensitivity to oxygen lack and the atmospheric level can fall from its normal 21 per cent to 13 per cent without noticeable effects; even then, though respiration is augmented and the victim becomes blue, there is no great distress and quiet collapse follows without warning, as happens to unmasked pilots flying at high altitudes. These chemical stimuli also act indirectly, but with the same results, on sensory nerve endings in the aorta and carotid artery.

2 The *nervous* or *reflex control* is effected by the great vagus nerve on each side of the body, which connects the vital centres of the medulla with the heart, lungs and abdominal organs. On the sensory side, these

provide the respiratory centre with information on the state of distension of the lungs and the blood-pressure and gaseous content of the great arteries. And on the motor side they carry down reflex responses modifying the action of the respiratory muscles accordingly. Gross examples of this mechanism are the inhibition of respiration following a blow on the larynx or solar plexus, and the violent expiratory efforts (coughing) caused by food entering the air-passages.

Of the two parts of the respiratory centre, the inspiratory one is dominant and the respiratory act is simply an active inspiration due to messages sent along the vagus nerves, with expiration succeeding as a passive relaxation due to falling-off in these stimuli. The ultimate co-ordination of the two is a very pretty example of reflex action. When inspiration is at its height the lungs are so inflated that their sensory nerve endings are greatly stretched ; they stimulate the expiratory part of the nervous centre, the vagus action is inhibited, and expiration follows, to cease in its turn when deflation is accomplished. In other words the very act of inspiration produces the necessity and the stimulus for the succeeding expiration ; it is as if a pair of bellows were fitted with an automatic electric control which made it absolutely certain that opening would be followed by closing ; and that, since the tendency from outside was always to open the bellows, a rhythmic opening and closing would be normal and automatic.

Thus the nervous control of respiration affects its rhythm, while the chemical control affects its depth ; and these are normally in collaboration, for obviously if increased carbon dioxide increases the volume of inspiration, it must also accelerate the stretch-response, and thus the nervous control of rhythm. In exercise, the rising of the level of carbon dioxide in the blood as a waste product of muscular activity reaches the brain and at first stimulates respiration. But as the effort increases, carbon dioxide is actually washed out of the blood by forced breathing, and the stimulus now comes from the lactic acid formed in muscular contraction and from the adrenaline secreted in excited states. It is this steady succeeding stage which is known as "getting one's second wind". Deliberate forced overbreathing at rest will so empty the blood of carbon dioxide that the normal stimulus to respiration is entirely removed; if one breathes in and out as forcibly as possible for a couple of minutes, it will be found that there is no wish to breathe and no actual breathing during the next couple of minutes; but the experiment is a little dangerous.

Oxygen Deficiency. A lack of oxygen available to the tissues may occur in many ways: by a lowered oxygen content of the atmosphere; by obstruction to the air-passages impeding the free entry of air; by lung disease preventing gaseous interchange; by inability of the blood to carry its full quota of oxygen, as in haemorrhage or anaemia, or when the haemoglobin is put out of action by combination with a poison such as *carbon monoxide*, or when the circulation is slowed as in heart failure; and by inability of the tissues in poisoning to utilize oxygen. All these conditions have the same result, an overbreathing resembling that due to exertion, but occurring at rest, in an effort to make up for the deficiency by increasing the intake of air; so that the cardiac invalid in his chair may be panting away as strenuously as a man who has just run a mile race. In all these states, the blueness of the insufficiently oxidized haemoglobin is evident in the lips and under the nails, the condition known as *cyanosis*.

Heights and Depths. Similar changes occur at increasing altitudes, on mountains or in aircraft; the oxygen available decreases as atmospheric pressure falls and reaches the danger point of 11 per cent at 16,000 feet, above which an oxygen mask is desirable. The immediate compensation is by overbreathing and by an increase in the rapidity of the circulation, though of course both these mechanisms fail at high levels. On the other hand, a more permanent adaptation can be made by mountain dwellers, who can acclimatize themselves at up to 15,000 feet by two means: an increase in the number of red blood corpuscles which may reach 8,000,000 per cubic millimetre, and an habituation of the tissues to a lowered oxygen content.

In working at depths, as with divers, or in compressed air, two factors come into play. The normal pressure of carbon dioxide is increased in the compressed atmosphere proportionately to the pressure and produces its usual toxic effects. At the same time the nitrogen, normally poorly soluble in blood, is driven into solution; and if the pressure is suddenly released, nitrogen is liberated in the blood as bubbles which may block the heart or nervous system and cause death or paralysis. Hence the necessity for gradual decompression in these cases; and divers suffering from the "bends" after being brought up too quickly must be treated by immediate recompression in a pressure chamber.

CHAPTER XI

MUSCLE

WE have already referred to the different types of muscle tissue (p. 23): *striped* or voluntary; the *smooth*, unstriped or involuntary; and the *cardiac* muscle of the heart. Excluding the last, there is a general distinction to be made between the striped muscles attached to the skeleton of the trunk and limbs and concerned with voluntary movements, controlled by the will through nervous messages from the brain, and the smooth muscle forming the walls of such hollow internal organs as the bladder and bowel and of the arteries and smaller blood vessels. The latter are required to function automatically and regularly without conscious attention, and are under the control of the semi-independent autonomic nervous system. Sometimes these two sets of muscles are referred to as the *somatic* muscles of the body wall and the *visceral* musculature of the internal organs.

Skeletal Muscle. The voluntary muscles differ essentially from the involuntary in that they normally only contract in response to environmental changes, this response being mediated by the central nervous system. Fig. 24 shows how a stimulus to such a sensory surface as the skin is conveyed by a sensory nerve fibre to the central nervous system, and is there relayed to a motor nerve cell whose fibre runs out to end in the muscle which it stimulates to contract. This is the primitive arrangement of the *reflex arc*, which is well established in quite simple animals, and has for its purpose the immediate and unthinking performance of such actions as withdrawal or blinking in protection from some noxious agent. In man, however, reflex actions have come increasingly under the control of the will, i.e., the message is simultaneously relayed up the spinal cord to the higher levels of the brain, which may so react as to modify the primitive response. The situation is comparable to that of a ship on the high seas, which is being steered by a gyroscopic compass responding reflexly to any change in course ; but the information from which is being constantly noted by the captain, who may intervene at any time to effect a deliberate alteration in position. Meanwhile, deep in the bowels of the ship, the engines are pounding away, using up fuel, expelling wastes and pumping out bilge water, and the captain is quite unaware of these internal processes, though he may modify them indirectly.

Every skeletal muscle has motor nerve fibres connecting it with the central nervous system, but it is also provided with sensory fibres carrying information as to the degree of contraction and the tension within the muscle ; this latter information is important, as muscles act in groups and in relation to each other, so that they require central co-ordination based on the knowledge of how they are all behaving.

Muscle Contraction, Tonus, Posture. An individual fibre contracts by some 50–60 per cent of its fully-stretched length, and either contracts this maximal amount or not at all—the " all-or-none " law ; but not all the fibres of a muscle necessarily act at the same time, the proportion depending on the actual work to be done. Muscle action moves the joint or joints lying between its origin and insertion, the former of these words meaning the fixed, and the latter the moving, attachment. This is clear enough when done against resistance, or against the mere weight of the limb. But, even when a movement is assisted by gravity, as when the arm is dropped to the side, there is a controlled *relaxation* ; in this case the arm-lifting muscles undergo relaxation, which is really a continuous readjustment of the degree of contraction ; i.e., " relaxation " is an active process. The ordinary contraction, when the origin and insertion are allowed to approximate freely and the muscle belly shortens adaptively, is *isotonic*, as the tension remains fairly constant throughout ; if the attachments are kept separated by some resistance, the muscle cannot shorten and its tension rises greatly, an *isometric* contraction of constant length. And since most actions are performed against some degree of resistance, contractions are usually a blend of isometric and isotonic.

Living muscle is never completely relaxed, except under deep anaesthesia, but is always in slight contraction or *tonus*. The state of the fibres is best expressed by comparison with a pianist continuously rippling over the notes of a piano ; some notes are always sounding at a given moment, but they are always changing. Tonus is essential to the maintenance of posture, especially the erect posture of man, as it holds the body against the collapsing strain of its own weight, particularly the feet and legs, whose ligaments would be subject to enormous deforming stresses were it not for the constant guarding tone of the surrounding muscles. And the spinal column is not a straight rod but a series of curves from above downwards, whose general shape is maintained by the long spinal muscles forming the chords of these arcs. Essentially, postural reflexes in the erect position are devoted to preserving an upright, forward-looking head, and a complex reciprocal action of all the main muscle groups in calves, thighs, buttocks, spine and neck exists to secure this end. Hence the necessity for a *sensory* nerve-supply from the muscles, telegraphing the exact state of tension from moment to moment to the central nervous system.

Muscle Groups and Movements. Muscles are usually found in groups with the same nerve-supply, acting to perform common or related actions. It is this movement, and not the individual muscle, that is represented in the brain, and no individual muscle can be contracted by an act of will. We try to lift our arm, not to contract our deltoid, though this is the main muscle concerned ; and a whole host of associated muscles come into play, most of them beyond the fringe of consciousness. In its relation to a particular movement an individual muscle may fill one of the following rôles :

(i) The *prime mover*, directly responsible for the actual movement.

(ii) The *antagonist*, which is capable of causing the reverse motion and therefore has to relax reciprocally as the prime mover contracts, actively paying out just enough slack to let the latter do its job.

(iii) The *fixators*, associated muscles steadying the base or fulcrum against which the prime mover acts.

(iv) The *synergists* act by controlling an intermediate joint so that the prime mover may act with maximal efficiency ; thus the muscles closing the fingers can only produce a strong grip if other, synergist, muscles simultaneously bend the wrist backwards.

And, of course, in connection with different movements the same muscle will play different parts.

Muscles may be artificially excited to contract by such insults as the application of heat, mechanical pinching, irritation with chemicals, or an electric current ; and the last is of particular interest to the experimental physiologist because the nature of the normal nervous stimulation of muscle is itself electrical. A constant galvanic current excites a single contraction at the beginning and end of its flow, i.e., at make and break ; a faradic current does likewise but the current is of much shorter duration and there is a minimum length of time of current-flow below which there is no response. This *threshold value* is only a fraction of a second in quickly-responsive warm-blooded animals, but may be several seconds in sluggish cold-blooded creatures. The effectiveness of response of a muscle to electrical stimulation rises with the strength of the current, and there is a minimum strength below which stimulation is ineffective. This increase of response is due to a larger number of individual muscle fibres taking part in the contraction ; but, as far as each fibre is concerned, each contraction in which it takes part is an all-or-none effort ; it contracts completely or not at all, and the greatest contraction a muscle can make is when all its component fibres are contracting. After contraction there is a short *refractory period* of a minute fraction of a second during which the muscle is inexcitable ; this is a period of recovery and preparation for the next contraction, and is of course an essential part of the cycle of cardiac muscle contraction as we have seen (p. 25).

If a muscle is repeatedly stimulated, it does not continue contracting indefinitely but becomes *fatigued* ; it does less work and eventually ceases to respond. This state of affairs is due to the using-up of all the food substances providing energy for the contraction, e.g., glycogen, and the accumulation of waste products, such as lactic acid. In combating fatigue, a plentiful supply of blood and oxygen is essential ; but fatigue in man is not just a simple matter relating to the muscle itself, but a more complex one involving the tiring out of the controlling nerve cells and fibres.

The tense generalized muscular contraction that occurs after death in *rigor mortis* must not be confused with ordinary contraction in life ; it is associated with the accumulation of lactic acid and an irreversible change in the muscle proteins. But it is accelerated by previous fatigue, so that it is very rapid in onset in animals which have been hunted to death.

The Biochemistry of Muscle. Muscle tissue is threequarters water, and the solid part is mainly protein. The muscle protein is very complex ; indeed the gross changes of contraction and relaxation, visible to the naked eye in the muscle as a whole, is the summation of a lengthening and shortening of the chains of atoms in the myriads of molecules constituting the muscle-proteins, a concertina-like process which is repeated on a vast scale.

Glycogen and lactic acid are also present, and we have already referred to the rôle of these substances in muscular contraction on p. 76. The glycogen is derived from the carbohydrate of the food and provides a source of energy for contraction, being converted in this process into lactic acid. Therefore, though the resting muscle contains only minute amounts of acid, it accumulates after repeated contraction, while the glycogen store is steadily used up. In the muscle itself the lactic acid is always normally neutralized as it is formed, or it would give rise to the local changes of rigor ; but some enters the blood-stream, and we have seen that its presence here in exercise stimulates the respiratory and cardiac centres to greater efforts, and that it is also taken up from the blood by the liver for reconversion to glycogen. A good deal of the lactic acid that remains in the muscle is restored to glycogen during the recovery period after contraction, but as much as one-fifth is burnt away to carbon dioxide and water by oxygen.

For this reason, an adequate supply of oxygen is essential to contracting muscle, which uses up ten times as much as in the resting state; the oxygen is needed not so much to enable it to contract, as to allow it to recover from contraction. A muscle stimulated to the point of fatigue in an inert gas such as nitrogen is incapable of such recovery.

The oxidative removal of excess lactic acid does not keep pace with its accumulation at the beginning of a continued effort, and its concentration in the blood rises. This is one of the main reasons for the breathlessness of exercise, an endeavour to increase the oxygen supply so as to get rid of lactic acid excess in the blood; and when a steady state is achieved at which the oxygen intake can deal with the acid at the rate it is formed, the individual has acquired his "second wind", and can continue comfortably for a long period. On the other hand, after a short period of very strenuous effort, one continues to be out of breath for several minutes afterwards as there is a dammed-up accumulation of lactic acid in the blood still to be oxidized; and the body is spoken of as having got into "oxygen debt" by accepting more calls on its oxygen supply than it can meet at the time.

A good deal of *heat* is produced during muscular contraction, largely in the process of lactic oxidation, and the sweating of effort is in order to lose this excess heat.

A brief note on the nature of the electrical wave-changes passing through a muscle when it contracts is to be found on p. 35.

Smooth Muscle. It is necessary to make some special remarks on this type of muscle, as it differs considerably from the voluntary muscle we have been considering, both in inherent properties and in nervous control. Thus it has an essential property of independent and rhythmic contractions ; and it is under the control of a different nervous system, which permeates the muscle tissue itself with nerve plexuses and clumps of nerve cells (ganglia) exerting a local control over contraction. Moreover, while the motor nerves reaching voluntary muscle from the central nervous system have only one action—to make it contract, the autonomic fibres supplying smooth muscle are of two kinds—sympathetic and parasympathetic—which stimulate it to relax and contract respectively. And as we have seen, these actions are reproduced powerfully by the effects on the muscle of certain chemical agents : adrenaline, which mimics sympathetic action ; and acetylcholine, which mimics the parasympathetic. Smooth muscle is much more sluggish in its response than voluntary muscle. It is particularly sensitive to stretching ; and this is important, since the hollow organs like the bowel and the bladder, which contain air and urine, are made of smooth muscle which needs to respond to distension or relaxation of the organ. A *slowly* increasing distension, as when the bladder steadily fills with urine, causes the muscular coat to relax proportionately, so that the pressure of the fluid does not rise until the last stages of great distension ; at this point the rising pressure stimulates the muscle to rhythmic waves of contraction, which end up in a mass contraction and expulsion of the contents of the organ. On the other hand, the *rapid* distension of a hollow organ provokes an immediate and intense spasmodic response.

The entrances and exits to hollow organs are controlled by specialized contracting circular bands of smooth muscle or *sphincters*, e.g., the cardiac and pyloric sphincters at each end of the stomach ; these are normally in a state of contraction until relaxation is necessary to allow the organ to fill or empty. It is obvious that the nervous and chemical control of a sphincter must be exactly the converse of that of the organ as a whole, since it must contract while the organ relaxes, and vice versa. So we find that the parasympathetic and sympathetic nerves, and the chemical agents which correspond to them, exert exactly the opposite actions on the muscular wall of an organ and the sphincter muscle which guards its exit.

CHAPTER XII

THE NERVOUS SYSTEM

All protoplasm is sensitive and responds to stimulation. This property is highly developed in nervous tissue, and the fibres which spring from nerve cells are specialized for the transmission of impulses, a largely electrical phenomenon. The nervous system of man can be re-

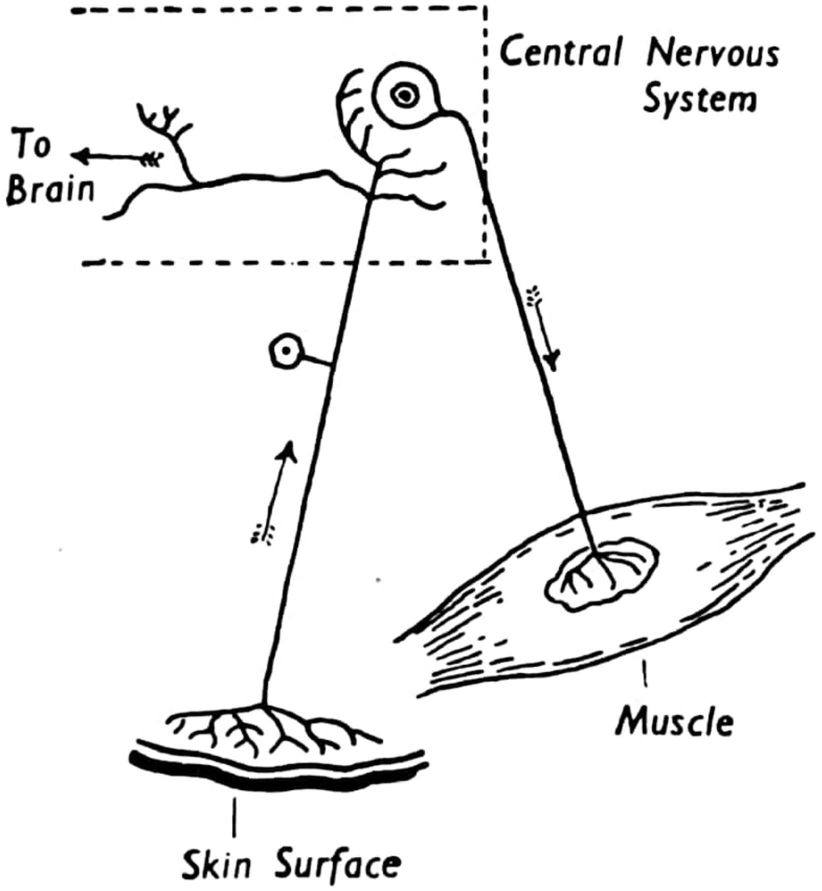

Fig. 24.—A simple reflex arc. The stimulus conveyed from the skin is relayed through a cell of the central nervous system to elicit an automatic contraction of the appropriate muscle. At the same time information is passed to the brain for conscious control of the proceedings.
(Adapted from Starling's *Principles of Human Physiology*.)

garded as a network pervading the whole body, having a two-way connection with the central control and enabling the individual to give a co-ordinated response to any stimulus from outside.

The *receptive* part of this system conveys such information as sight and touch from the outer world to the controlling nerve centres; but it also provides information as to the state of the body and internal organs. Some of these messages enter consciousness, giving us our conception of the universe; others, notably those from within us, remain largely unconscious, though they help to regulate the normal working of the body.

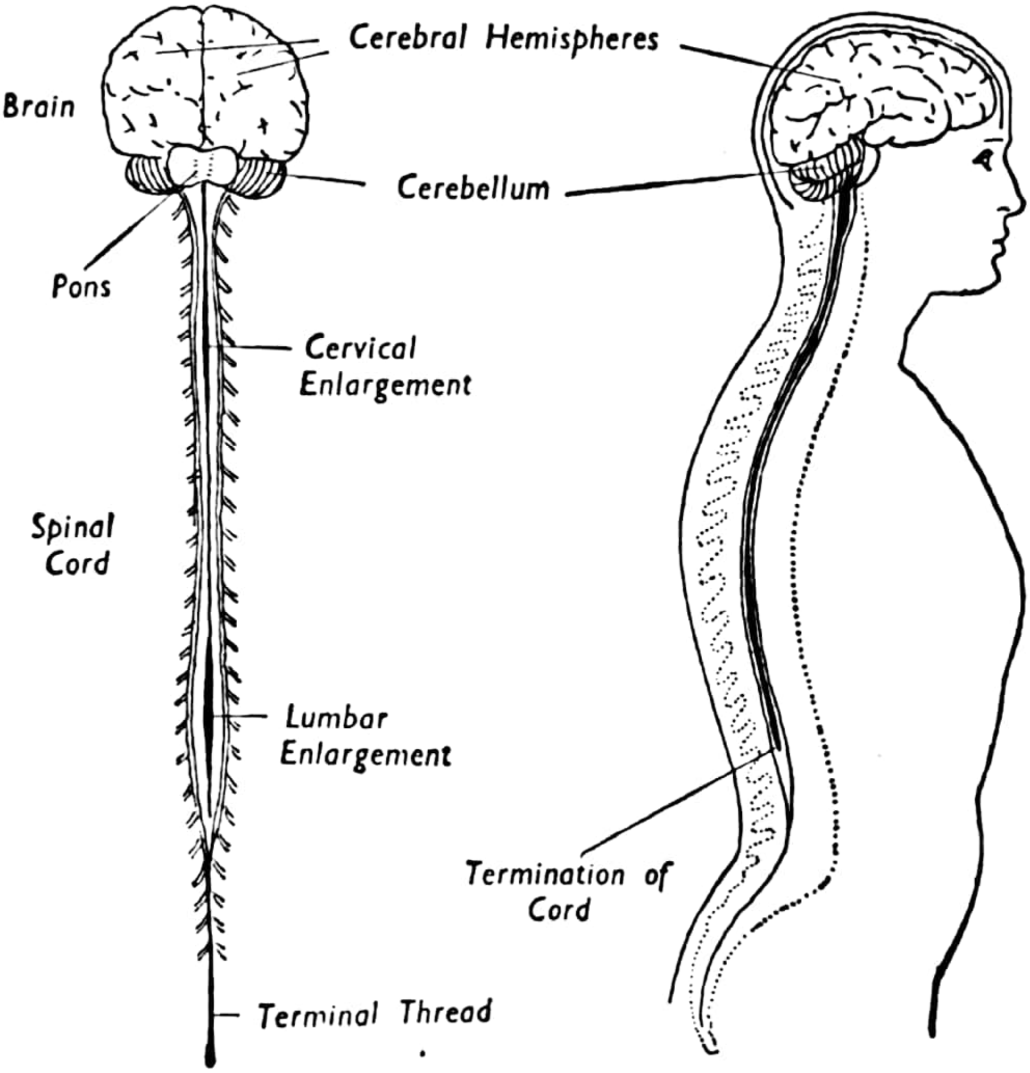

FIG. 25.—The central nervous system.

The *emitting* part of the nervous system carries messages out from the nerve centres, to produce changes in the *effector organs*—muscles and glands ; and this response is meant to deal with the situation provoking the original stimuli. In fact, from the purely physiological view (though not necessarily the philosophical) the brain is nothing but the centre of a glorified reflex arc. It does nothing actively, except in automatic response to outside stimulation ; so-called voluntary movement is merely the result of some provocation of which we may be unaware, and consciousness is merely an incidental by-product of the whole complicated arrangement.

The Nature of Nervous Transmission. A nerve fibre is the elongated process of a nerve cell ; the elongation may be enormous, e.g., the fibres of the sciatic nerve run for several feet from the toes to their microscopic cells of origin in the lumbar region of the spinal cord. The fibres are bound together in bundles, and these in turn are grouped by connective tissue packing into one large bundle, the main nerve trunk. In those nerves derived from the brain and spinal cord each fibre has a fatty insulating sheath ; this sheath is absent from the finer fibres of the autonomic nervous system.

Though the nerve fibres are sensitive to direct stimulation, they normally only *conduct* stimuli, either those passing out from the central nervous system to the muscles and glands, or those travelling in from the skin and sense organs to the brain and cord. These impulses, then, originate at either terminus of the fibres, and fibres normally conduct only in one direction because of their particular connections, and not as an essential property. If we graft a portion of sensory nerve into a gap in a motor nerve, the graft will conduct impulses quite efficiently in the reverse direction from that which it used to do. Thus nerves are comparable to telephone wires; the nature of the conversation conveyed depends only on who happens to be connected at either end. Thus, too, we associate the optic nerve with sight and the olfactory nerve with smell, but they serve these particular functions only because they link the appropriate sense organ with the corresponding area of the brain; in themselves, the impulses transmitted are identical with those carried by nerves in general.

Nerve fibres are readily stimulated experimentally, electrically or by pinching, and stimulation sets up a wave of negative electrical potential travelling along the nerve at the rate of some 300 feet per second. This electrical wave is not in fact the nerve impulse itself; it is merely a measurable record of the underlying disturbance, itself obscure. There is some distinction between the large sheathed motor and sensory fibres of the central nervous system, which carry impulses at a velocity of 300 feet per second, and the fine fibres of the autonomic system where the speed is only some 5–50 feet. These differences are related to the necessity for immediate response to an external situation, whereas the regulation of the internal organs is a more leisurely process.

Nervous action is essentially a stream of such small, discrete, separate impulses, repeated at very short impulses like a burst of machine-gun fire; there is no such thing as a *continuous* flow of nervous excitation. And there is a maximum rate for such a stream, since each impulse is followed by a short *refractory period* during which the nerve will not transmit a succeeding stimulus.

In its activities nervous tissue undergoes metabolic changes in exactly the same way as the body tissues generally, using up oxygen and liberating carbon dioxide, with the evolution of heat. The quantities involved are minute compared with those concerned with, say, muscular activity, but they are none the less essential. Nervous tissue, particularly the cells of the brain, cannot tolerate deprivation of oxygen for more than a minute or two ; and this is the reason for the serious damage to the brain which may follow temporary cessation of the heartbeat during an operation, damage which is often permanent even if the heart is restarted efficiently.

As far as a single nerve cell and its fibres are concerned, the nervous impulse is conducted smoothly and continuously ; but there is an inevitable break when the impulse is relayed by another cell-unit. Such relays or *synapses* are common in the nervous system ; motor impulses coming from the brain are relayed by fresh cells in the spinal cord whose fibres run out to the muscles, and sensory impulses from the skin are relayed by other cells in the cord, before being transmitted up to the brain to reach consciousness. Every relay implies a breach in anatomical continuity ; the incoming fibre ends in a network of branches which embrace the new cell but do not blend with it. The whole complex of a nerve cell and its branches is known as a *neurone*, and the nervous system is made up of millions of such neurones, connected with each other at these relays or synapses. Because of the breach in physical continuity, messages are delayed a little at the synapses, just as a call made along a telephone and its extended wire is delayed at the central exchange, while the operator plugs it in to its destination. The bridging of the physical gap between one neurone and another is effected by chemical means ; the branching nerve endings liberate chemical substances, which stimulate the adjacent cell to start off a fresh impulse down its own fibre. Thus nervous activity is a complex blend of electrical conduction along the fibres, and chemical excitation at the synapse-bridges. A similar gap must be crossed when a motor nerve fibre ends in its muscle, and this again is achieved by liberation of a chemical agent. Though nerve fibres can conduct in either direction, the transmission at the synapses themselves is strictly one-way and sets the pattern for the flow of impulses in the central nervous system ; and the same applies to the nerve-muscle junction which is designed only to permit a flow of impulses into the muscle fibres.

Although in the nervous system chemical agencies are subsidiary to the neuronic control, these substances are very potent and will produce the same ultimate effects in certain organs if injected independently into the blood-stream. When we come to consider the autonomic nervous system, we shall see that chemical agencies play a very large part in regulating the internal organs and blood vessels, and that there is an accessory arrangement by which special glands (e.g., the adrenals) can secrete their hormones directly into the blood in order to secure a rapid response in an emergency.

The Anatomy of the Nervous System. The controlling nerve centres of the body make up the *cerebrospinal* or *voluntary nervous system*, which is mainly concerned with the movement and sensation of the somatic or body-wall structures—skin, muscles, bones and joints—though many of its activities are far from conscious. In contradistinction to this, there is the semi-independent *autonomic* or *vegetative nervous system*, which deals with the automatic functioning of the viscera, the internal organs, and of the glands and vessels. Obviously the two systems are closely interconnected, as we shall see.

Voluntary Nervous System. The brain is enclosed in the bony cranium, and the spinal cord within the spinal column ; they are continuous with each other where the cord enters the base of the skull through a large aperture, the *foramen magnum.* Brain and cord together make up the *central nervous system* or *cerebro-spinal axis.* The 12 pairs of cranial nerves arising from the brain and the 31 pairs of spinal nerves arising from the cord constitute the *peripheral nervous system.*

The Spinal Cord

The elongated cylindrical cord extends from the base of the skull to the first lumbar vertebra, and is marked by two ovoid swellings, the *cervical* and *lumbar enlargements*, which are the sites of origin of the nerve plexuses which supply the arm and leg. In the foetus, the cord occupies the whole length of the spinal canal ; but failing to keep pace with the growth of the spine, it

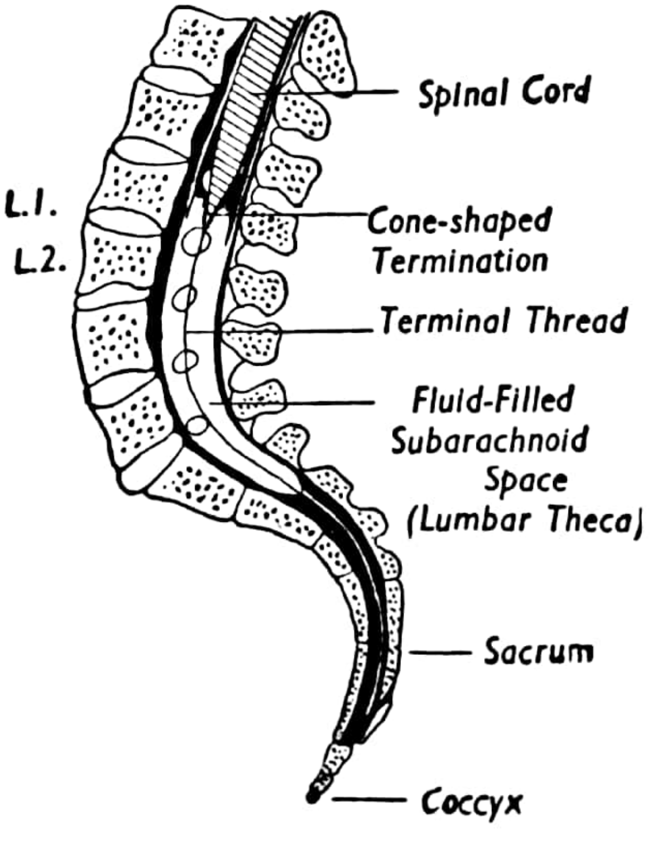

FIG. 26.—The termination of the spinal cord in the upper lumbar region. (After *Gray.*)

gradually recedes, ending in the adult as a conical extremity at the first lumbar vertebra. Now, the lower lumbar and sacral nerve roots still emerge from the bony spine at their correct levels between the vertebrae ; thus, they have to run increasingly obliquely down and out, as the bony spine lengthens in relation to the cord ; so the spinal canal, below the end of the cord, is filled with a mass of roots descending to their appropriate lumbar and sacral exits. Because of this recession of the cord with growth, its lumbar enlargement is actually in the lower thoracic region.

Cross-section of the cord (Fig. 28) shows the inner H-shaped arrangement of *grey matter*, a mass of nerve cells ; and the surrounding *white matter*, made up of bundles of nerve fibres ascending and descending between cord and brain. In the very centre is a minute canal. On each side, the grey matter projects in front and behind as the bulbous *anterior* and *posterior horns*. The *anterior horn* contains the motor nerve cells, whose fibres are destined for the stimulation of muscles, and these leave the cord in a bundle as the *motor nerve root*. The *posterior horn* contains sensory cells ; they receive fibres through a *sensory root*, on which is situated a knob or *ganglion*, a sort of relay station. The two roots soon join up to form the complete spinal nerve emerging from the particular segment of the cord ; this leaves the spinal canal between the appropriate two adjacent vertebrae. Thus the spinal nerve contain mixed motor and sensory fibres, which are not separated out again until, in the ultimate peripheral distribution of the nerve and its branches in limb or trunk, specific motor and sensory twigs are given off to supply particular muscles or areas of skin.

It should be noted that our cross-section of the cord is much the same in appearance whatever the level of the section, i.e., the spinal cord may be regarded as consisting of a number of identical *segments*, to each of which is attached a pair of spinal nerves ; and each spinal nerve emerges by two roots on either side. This is a relic of the primitive segmentation pattern of the whole body, which is very obvious in such an animal as the earthworm, in which each segment exactly reduplicates the next and each contains its own essential organs. This pattern, though obscured in man by the development of head and limbs, lingers on in the repetitive arrangement of the ribs, the vertebrae, and in the structure of the cord itself. It is of particular importance in the latter, because each cord segment controls the sensation of a particular area of skin surface and the movement of a particular group of muscles ; these together make up the corresponding body segment, still retaining its fundamental connection with a particular segment of the nervous system, though the pattern is grossly distorted by evolution. Thus the sensation of the little finger is always supplied by the first thoracic segment of the spinal cord ; the muscles straightening the knee always derive their motor nerve fibres ultimately from the third and fourth lumbar segments ; and so on for every part of the body.

This constancy in innervation is of the greatest value in helping to locate the precise site of injury or disease of the central nervous system, because we can deduce from the particular muscles paralysed, or areas of skin surface devoid of sensation, exactly what the level of the disease process in the cord must be.

In the thoracic region the peripheral nerves follow the simplest segmental pattern ; each encircles the chest in its appropriate rib-space, without any connection with its neighbour above and below. But the lower nerves of the neck, and all those of the lumbar (loin) and sacral (buttock) regions, form complex networks as soon as they have left the spine; from these *plexuses* emerge the main nerves of the limbs, e.g., the median nerve in the arm and the sciatic in the leg, and these again are usually both sensory and motor in function.

The Reflex Arc has already been briefly referred to on p. 141. It is obvious that the spinal cord provides a relatively simple means for the performance of certain primitive and essential actions, without the intervention of the brain. Thus, an irritation of the skin sends a sensory impulse through the posterior root to the posterior horn of the appropriate segment; this is relayed to the anterior horn cells of the same segment of the cord and becomes a motor impulse travelling out through the anterior root to activate muscles which remove the affected part from the noxious agent. This is the reflex arc at its simplest, the so-called withdrawal reflex; it is the only pattern of action in the lower invertebrates and it is independent of the brain, though the brain is aware of its results and can to a certain extent modify them. On a more complex level, but basically similar, are the reflexes of micturition, defaecation, sexual orgasm and childbirth, all controlled by a particular segment or group of segments of the cord; and all these reflexes can still take place, even when the cord-brain link is completely severed by injury so that the lower part of the body is paralysed as far as conscious sensation and movement are concerned.

Interconnections in the Spinal Cord. The grey matter of the cord is composed of nerve cells, with short fibre connections at the same transverse level. The white matter is made up of bundles of fibres running longitudinally up and down the cord in cable fashion, and these are grouped into a constant pattern of individual *tracts*, some of which are sensory and some motor.

These run between cord and brain and link the anterior or posterior horn cells with the appropriate controlling or receptive areas of the brain. Thus, from that part of the cerebral cortex controlling arm movement fibres run to the anterior horn cells of the seventh cervical segment of the cord ; here there is a synapse relay, and from those cells fibres leave in the motor root, run out in the seventh spinal nerve, and activate the muscles bending the wrist. Or again, sensory impulses from the knee travel up the limb in the femoral nerve, through the leg plexus of spinal roots, and via the fourth lumbar nerve into the fourth lumbar segment of the cord ; here they are relayed to other cells whose fibres run up the cord in a long sensory tract, travelling to the sensory area of the brain. All levels of the brain are concerned either as termini or starting points ; at the highest level is the cerebral cortex, where impulses enter consciousness ; and lower down in the brain-stem are the mid-brain and hind-brain which regulate automatically posture and internal activities. But an invariable principle is, that at some point, usually in the brain-stem itself, the fibre tracts *cross* from one side to the other completely, so that the sensory and motor regions of the brain control the opposite half of the body.

The Brain

The brain is the greatly expanded and elaborated upper end of the cerebrospinal nervous axis ; it fills almost entirely the cranial cavity. But, despite its continuity with the spinal cord, in it the arrangement of grey and white matter is exactly the reverse of that in the cord, for the grey matter is now on the surface and the white fibre tracts within.

From above downwards, the main parts of the brain are as follows :

1. The Fore-brain is the great overhanging pair of *cerebral hemispheres*, making up the bulk of the brain. They are symmetrical rounded masses of convoluted nervous tissue, which completely hide the lower parts of the brain when viewed from above. Each hemisphere is connected with the other by a great bridge of fibres. The superficial grey matter or *cerebral cortex* has an enormous area owing to the intricacy of its convolutions; the increasing complexity of this pattern in evolution, through the vertebrates to man, is a measure of the increase in intelligence and consciousness.

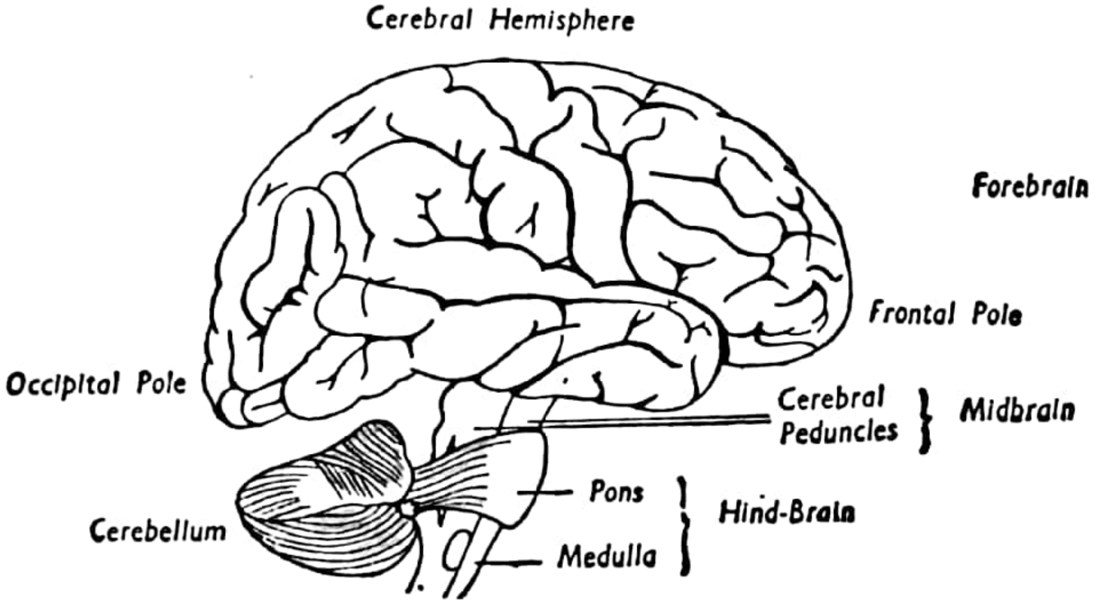

FIG. 27.—The brain in side view. Diagrammatic. (After *Gray*.)

Each hemisphere is composed of several lobes; a *frontal* lobe at the forehead end, an *occipital* lobe behind, with intervening *temporal* and *parietal* lobes. Each of these has its own particular functions and the localized areas associated with particular activities are indicated in Plate 4. The main *motor* and *sensory areas* are placed midway between the poles of each hemisphere; they are relatively small strips of cortex, on which the whole body is, as it were, projected, but in inverted fashion with the leg area uppermost, head and neck centres lowest. All these functional areas are concerned with the opposite side of the body, but with certain modifications in the case of sight and speech. The *visual area* in the occipital lobe is not concerned so much with the opposite eye as with gathering all the visual impulses from the opposite field of vision which have entered *both* eyes, and this arrangement is shown in Plate 3. The *speech area* affords the only example of one-sidedness in the brain, for it is situated in the *left* temporal lobe and with it is associated appreciation of the meaning of spoken, written, read and heard words ; this arrangement is linked with the predominance of the right hand, and in left-handed people the speech centre is in the *right* cerebral hemisphere.

It will be seen that much of the cerebral cortex is assigned no special function. These are the psychic or *association areas*, concerned with the interrelating of sensory and motor data and with the higher levels of consciousness and personality, particularly in the frontal lobes. The frontal lobes may be destroyed or removed without interfering with essential cerebral activities, though with considerable changes in mood and the capacity for self-appraisal.

Although this account of cerebral localization of function suggests a very precise division of labour between the different regions of the fore-brain, in fact there is some power of one area to compensate for another lost by disease or injury, though this is never very great in man. Man's power of associating linked impressions and ideas represents the highest development of mental processes in the animal kingdom. It takes place mainly in the large areas of cortex to which no particular motor or sensory function can be assigned, and on it depends his educability and capacity to learn from experience.

Cross-section of the fore-brain (Fig. 36, p. 187) shows the surface pattern of convolutions, the contrast of grey and white matter, and the cleft between the hemispheres; it also shows the hollow fluid-filled chamber or *ventricle* in the depths of each hemisphere, with surrounding masses of grey matter—the *basal ganglia*, which may be intimately connected with the emotions.

2. **The Mid-brain** is deeply placed at the base of the cerebral hemispheres and its main mass is a squat *cerebral peduncle* on either side, a pillar supporting the corresponding hemisphere and carrying fibres to and from it. In the roof of the mid-brain are the nerve cells controlling the movements of the eyes; and from its floor a little pea-like body projects down—the *pituitary gland*, the most important of the organs of internal secretion (p. 191).

3. **The Hind-brain** is best seen on the underside of the organ. It comprises:

(i) The *medulla oblongata*, a bulbous expansion formed by the direct continuation of the spinal cord into the skull.

(ii) The *cerebellum*, a pair of finely-convoluted miniature hemispheres.

(iii) The *pons*, a broad bridge of fibres connecting the cerebellar hemispheres. This is above the medulla and below the mid-brain.

From the point of view of evolution, the hind-brain is the oldest and most primitive part of the organ and is concerned with maintaining the basic activities of the body; it is largely independent of conscious cerebral control and continues to function fairly normally even when sleep, unconsciousness or deep anaesthesia have put the fore-brain temporarily out of action. The medulla contains the vital centres which regulate the heartbeat, respiration and blood-pressure; and these, in injury or disease, remain active until the last moment before death supervenes. The cerebellum is concerned with the regulation of muscle tone and posture, and does so in response to the changing sensory impulses of position and tension it receives from joints and tendons, and also from information gained as to the body's position in space from the semicircular canals of the ear. That is to say, it is concerned with the essential postural mechanism of the head and trunk, the automatic righting reflexes which restore the upward carriage of the head after an upset of balance.

We may regard the brain in general as a series of cell-stations situated at higher or lower levels, in the grey matter of the cerebral cortex, the basal ganglia, the mid-brain, medulla and cerebellum. To and from these cells great tracts of nerve fibres ascend and descend within the central white matter of the *brain-stem*, the axial conducting core of medulla and mid-brain. We have already encountered these tracts in the cross-section of the spinal cord. They may be classified as *motor* (descending) and *sensory* (ascending), and at some level, usually in the hind-brain, their fibres cross to the opposite side so that the functional areas of the brain represent the opposite half of the body. The main bundles are as follows (Plate 4):

Motor. (i) *Pyramidal*, running from the cerebral motor cortex to the anterior horn cells of the cord at all levels, and thence relayed to the motor roots of the spinal nerves; concerned with voluntary motion.

(ii) *Cerebello-spinal*, running from the cerebellum to the anterior horn cells, concerned with the automatic regulation of tone and posture.

Sensory. (i) The cord bundles carrying *touch* and *sensation* to the cerebral sensory cortex.

(ii) The bundles carrying *pain* and *temperature* appreciation to the cerebrum.

(iii) The spino-cerebellar tracts, conveying *sense of position* to the cerebellum.

All these sensory bundles are relaying impulses which have entered the cord via the sensory roots to the posterior horn cells. Since the sensory tracts acquire an increasing influx from higher roots as they ascend, and since the motor tracts must shrink in their descent as they shed fibres to successive segments of the cord, the bulk of the cord as a whole tapers from above downwards.

Membranes of Brain and Cord; Cerebro-spinal Fluid (Fig. 28)

Brain and cord have three enveloping membranes which are pierced by the nerve roots on their way out.

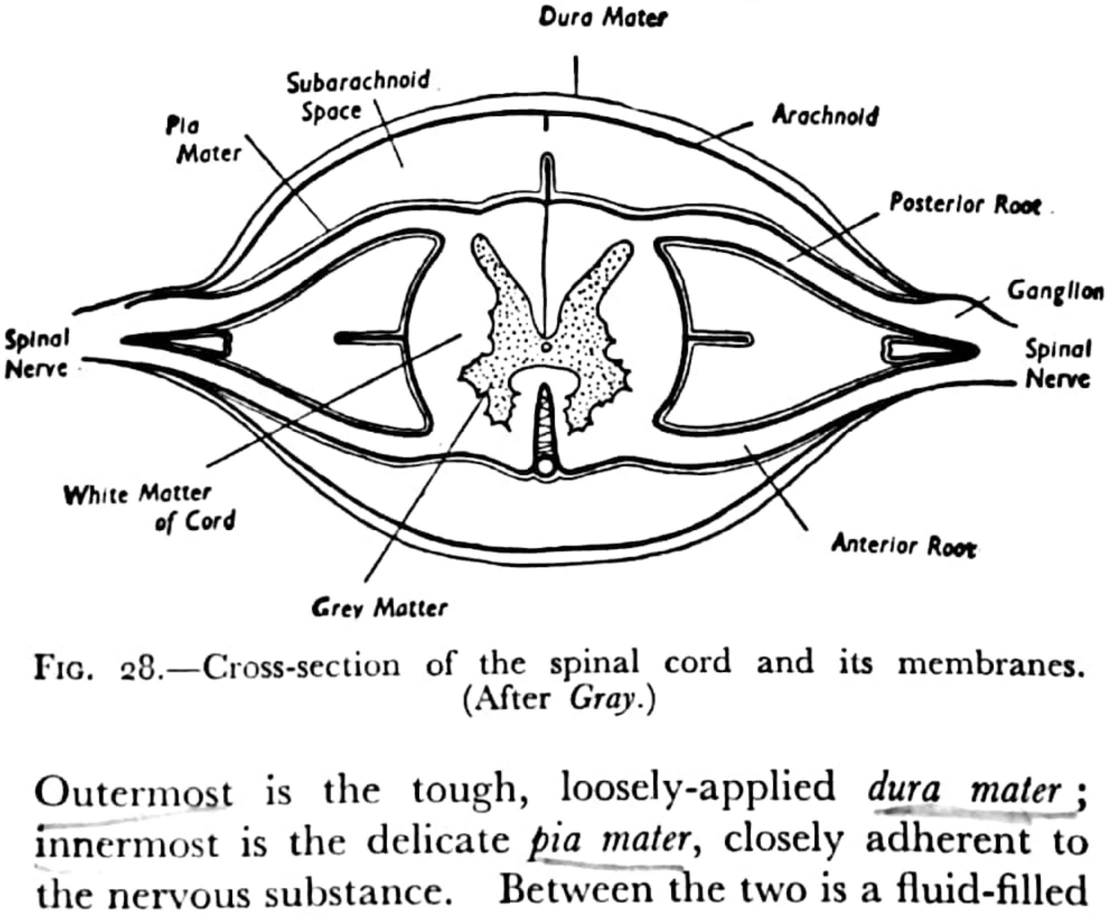

FIG. 28.—Cross-section of the spinal cord and its membranes. (After *Gray*.)

Outermost is the tough, loosely-applied *dura mater*; innermost is the delicate *pia mater*, closely adherent to the nervous substance. Between the two is a fluid-filled space traversed by the spidery meshes of the *arachnoid layer*. Although the spinal cord ends at the level of the first lumbar vertebra, its membranes are continued down as far as the sacrum ; and thus the lumbar portion of the vertebral column encloses a space or *theca*, filled with cerebrospinal fluid. This space can readily be entered by means of a long needle, inserted in the small of the back, and fluid thus obtained gives valuable information helping in the diagnosis of many diseases.

This *cerebrospinal fluid* bathes freely the outer surface of the brain and cord, cushioning them within the bony cranium and spinal column against any concussion. Furthermore the brain itself is hollow, traversed by a system of communicating chambers or ventricles, and so is the spinal cord which possesses a narrow central canal. All these spaces are filled with the same fluid, which is in continuous circulation, carrying nutriment to the nerve cells and removing wastes. The cerebrospinal fluid is secreted within the ventricles, escapes through several minute apertures in the roof of the hind-brain, and makes its way to the cranial vault to be reabsorbed into the blood-stream. It is normally maintained at a constant pressure, to support the soft bulk of the central nervous system ; this pressure is intimately related to the pressure of the blood in the great veins, and is raised accordingly when the venous tension is increased by coughing or straining. Any disease process or tumour within the unyielding box of the cranium greatly increases the cerebrospinal fluid pressure as it progresses, and this causes headache, vomiting, and ultimately severe disturbance of cerebral function ending in coma.

The Cranial Nerves. Just as the horns of grey matter in the spinal cord give off the roots of the spinal nerves, so in certain parts of the brain there are collections of nerve cells forming the nuclei from which spring the twelve pairs of cranial nerves, best seen on the underside of the brain. These are mostly concerned with movement and sensation in the head and face, including the eye, ear and nose ; but one (the eleventh) controls certain neck muscles, and another (the tenth or vagus) is distributed widely to the internal organs of the neck, chest and abdomen. They may be listed in order of their origin from the different levels of the brain, from above downwards.

Cerebrum. 1. The *olfactory* nerves transmit the sensation of smell from the mucous membrane of the nose to the fore-brain. It should be noted that much of what is usually regarded as taste is in fact accomplished through the appreciation of odours, as evidenced by the damping effect on appetite of a cold in the nose.

2. The *optic* nerves are concerned with sight ; each forms the stalk of an eyeball and gathers up fibres from the nerve cells of the retina. But these fibres cross over within the cranium, in such a way that each optic tract (the continuation of the optic nerve beyond the point of crossing) running to the visual area of right or left occipital lobe of the brain carries only fibres from the right or left halves of each retina, and not just the fibres from one eye as such. This separating out is essential to maintain the principle of one-sided representation of function in each half of the brain. For though the eye itself is a one-sided organ, it sees on both sides of the body ; what is needed for efficient co-ordination is that the whole of one side of the visual field should be represented as such in the cerebral cortex. Plate 3 makes this clear and shows how the right occipital cortex, for instance, receives all the impulses from the left field of vision, and vice versa.

Mid-brain. 3. The *oculomotor* nerves control four of the six small muscles moving the eyeball.

4. The *fourth* nerve controls another of the ocular muscles.

Hind-brain. 5. The *trigeminal* nerve is a large one, carrying sensation from the whole of the face and jaws and from much of the scalp, and supplying the muscles of mastication.

6. The *sixth* nerve controls the last of the six ocular muscles.

7. The *facial* nerve activates the facial muscles of expression, stimulates the secretion of some of the salivary glands, and carries taste sensation from the front of the tongue.

8. This is the *auditory* nerve, connecting the internal ear with the hind-brain. It is really double, serving two distinct functions. Its *acoustic* portion carries the sensation of sound and pitch from the cochlea, the true organ of hearing, and this is relayed to the auditory area of the cerebral cortex. The *vestibular* portion conveys sense of position and orientation in space from the semicircular canals of the ear, the organs of balance, to the cerebellum ; it provides constant information which aids the maintenance of equilibrium in the upright position.

9. The *glossopharyngeal* nerve carries sensation from the pharynx and tonsils, and taste sensation from the back of the tongue ; it also controls some small muscles associated with the pharynx in swallowing.

10. The great *vagus* nerve is important and complex, running down through the neck and thorax to the abdomen ; it is an essential part of the autonomic system which controls the internal organs and is therefore a link between this semi-independent system and the cerebrospinal axis. Its main branches are :

(i) In the *neck*, for movements of pharynx and larynx in swallowing and speech, and for sensation from their lining mucous membranes.

(ii) In the *chest*, it modifies heart action through the cardiac plexus ; carries sensation from the lungs via the pulmonary plexus ; activates the smooth muscle of oesophagus and bronchi and their associated glands, and carries sensation from their mucous linings.

(iii) In the *abdomen*, it supplies the muscles, glands and mucous membrane of the stomach, duodenum and small intestine, and sends twigs to liver, spleen and kidneys.

11. The *accessory* nerve supplies the muscles of the soft palate and larynx, and certain large neck muscles.

12. The *hypoglossal* nerve controls the muscles of the tongue and floor of the mouth.

Spinal and cranial nerves resemble each other in certain essentials. Motor fibres, whether springing from brain or cord, pass out without a break to their destined muscles. But sensory fibres travelling inwards always end at a group of cells situated just outside the cerebrospinal axis : these cells make up the *ganglia*, knobby swellings on the posterior spinal roots and on the sensory cranial nerves within the cranium ; it is the processes of these ganglion cells, and not the original sensory fibres, which ultimately enter the central nervous system. In other words, motor impulses are direct, but sensory impulses are mediated.

Autonomic Nervous System

The autonomic nervous system is distributed to the *viscera*—the hollow internal organs—and to the blood *vessels* ; it controls their smooth musculature and, where these are present, the secretory activity of the associated glands. Because all its nerve fibres are ultimately derived as an outflow from the cerebrospinal axis itself, it is analogous to a Local Authority in more or less complete control of sewage and transport arrangements, but only in virtue of powers delegated to it by Government itself. And these arrangements are susceptible to indirect modification by that Government, not through an act of will, but by means of the conscious or subconscious moods and emotions which strongly influence visceral activity.

The system contains two complementary parts, the *sympathetic* and *parasympathetic*, which are anatomically and functionally different. Both supply the viscera and vessels; their influence is mutually antagonistic; and it is associated with the liberation at their nerve endings in the organs of specific chemical substances: *adrenaline* in the case of the sympathetic, *acetylcholine* with the parasympathetic.

The effects of the sympathetic system are those of great bodily activity and preparation, in relation to the primitive reactions of fear and flight. It constricts the cutaneous vessels, raising the blood-pressure and shunting more blood to heart and brain; speeds the heart-beat; dries up glandular secretion; and relaxes the walls of the hollow organs while tightening their sphincters, thus allowing them to fill. In contrast, the parasympathetic deals with more constructive building-up activities in times of tranquillity. It dilates the peripheral vessels, lowers the blood-pressure and decelerates the heart; excites secretion; and empties the hollow organs by relaxing their sphincters and contracting their walls.

Nevertheless this generalization of the actions of the two parts is not so simple and clear-cut; the two parts of the system are in fact in complex and reciprocal control of the internal organs, though one or other may predominate in the same individual at different times, or in the same individual at all times, as in markedly placid or anxious types. To pursue our analogy, we can imagine a Local Authority employing builders who both make new houses and knock down old ones, but whose activities overlap at many points and require constant co-ordination.

Anatomical Arrangements (Fig. 29). The basis of the *sympathetic system* is a chain of ganglia, running the length of each side of the spinal column from one end to the other. The most typical arrangement is found in the chest, where there is one sympathetic ganglion to each spinal cord segment and spinal nerve. The outflow from the central nervous system to the sympathetic is by a little communicating twig from each spinal nerve to the corresponding sympathetic ganglion ; and from the ganglion the peripheral sympathetic distribution is effected in two ways :

(*a*) By a returning twig to the spinal nerve, its fibres travelling with it to the somatic structures of the body wall, there reaching the small vessels.

(*b*) By the formation of *sympathetic plexuses*, from which branches form a network around the vessels travelling to the viscera, e.g., the cardiac and pulmonary plexuses of the chest ; and the splanchnic nerves run down from the sympathetic chain in the chest to join the *solar plexus* just below the diaphragm, whence arises the whole sympathetic supply to the abdominal organs.

The *parasympathetic system* is less obviously separate, for its fibres are merely contained in certain cranial and spinal nerves at either end of the cerebrospinal axis ; the former supply the glands and vessels of the head, the latter the bladder, rectum and genital organs. But the tenth cranial nerve—the *vagus*—is the great parasympathetic trunk of the body, traversing neck, chest and abdomen to supply the viscera.

The ultimate sympathetic and parasympathetic twigs

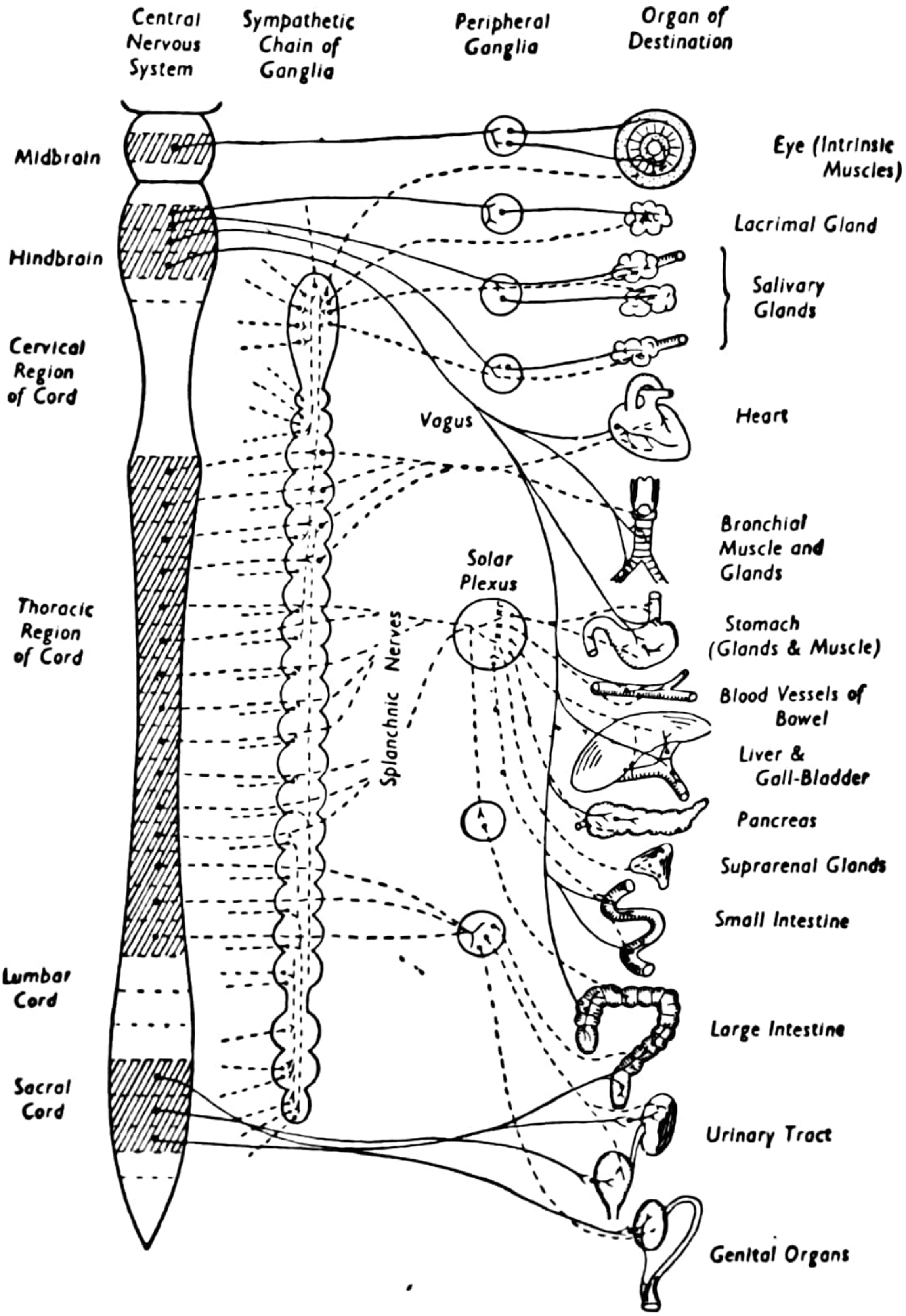

FIG. 29.—Plan of the autonomic nervous system. (After *Gray*.)

to the individual organs are often distributed in common, and are always interrupted by a synapse-relay at a peripheral ganglion before reaching their destination.

Conditioned Reflexes

In describing the essential process of the reflex arc, the examples quoted were instances of inborn or *unconditioned reflexes*, natural responses such as salivation on taking food, which develop quite independently of any special experience or training. Even the most complicated sexual and postural reflexes are inherited in this way and form the basis of the natural instincts. In contrast to these are the acquired or *conditioned* reflexes, peculiar to the individual and developed by him in adaptation to the circumstances encountered in his own life history. Thus it is *not* natural for one's mouth to water at the mere sight of food ; it is an acquired reflex, based on the general experience that seeing food is followed by eating it. So it is that everybody develops his own conditioned reflexes which are, however, usually widely shared because human experiences are so identical.

This development is only possible because of the extensive development of mental association in the higher animals. The acquired or conditioned reflexes are based on natural and inherited responses. Our mouths must water on taking food, for that is the way we are made, and the response has been determined even before birth. But if we learn to associate the sound of the dinner gong with the inevitable sequence of a meal, we eventually come to salivate at the sound of the gong alone, without needing the physical stimulus of the food in the mouth.

It is obvious that established conditioned reflexes may form the basis of still further acquisitions, and an enormous part of human behaviour is composed of such complex responses. These reactions can be facilitated or inhibited by changing or confusing the appropriate stimuli, but they are not inherited. The new-born child must start again at the beginning.

Sleep. All animals have a daily rest period, during which the activity of the body generally, and of the central nervous system in particular, is reduced to a minimum. During sleep there is considerable general muscular relaxation and movements are quietened down ; many of the reflexes disappear, the pulse slows and the blood-pressure falls, and metabolism generally is depressed.

From the psychological point of view the essential feature of sleep is the removal of the inhibiting control of the cerebral cortex over thoughts and ideas, so that dreams come to represent, albeit in masked form, the basic conflicts and desires of the unconscious mind. Very little is known of the real causes and control of sleep, apart from the general need of all tissues for recuperation after fatigue. It might almost be regarded as the natural condition once outside stimulation is reduced to the minimum, were it not that sleep is possible in exhausted states when the craving defies the most obtrusive stimuli. One thing is clear ; either as cause or consequence, there is a reciprocal relation between sleep and muscular relaxation and the latter is an indispensable preliminary. If anxiety causes persistent tension, sleep is impossible, and much insomnia is due to this cause.

The Sense Organs

We have seen that a large amount of sensory information from the muscles, joints and internal organs is constantly arriving at the brain ; but, with the exception of pain, these messages do not enter consciousness. Contrasted with this are the special sense organs : the eye, ear, nose, tongue and skin ; and these provide information of a very definite and particular quality and elicit rather complex responses. In discussing the nerves it was pointed out that the particular nature of a sensation is determined by the receiving organ, and not by the stimulus. This means that the same physical cause will produce different effects when applied to different sense organs, e.g., radiation of a certain wave-length is appreciated as light by the eye but as warmth by the skin, a tuning fork is only a repeated touch to the skin but conveys a note to the ear. And conversely a sense organ can only react in the one way, whatever the stimulus ; the eye not only reacts to light normally, but also transmits the sensation of light when the eyeball is pressed vigorously.

Another characteristic phenomenon in the relation between brain, sense organs and the outer world is that of *projection.* Though sensations are only appreciated as the result of changes in the brain cells, they are felt as if taking place more remotely ; touch is projected to the skin surface, taste to the mouth, while we regard sight and sound as coming from the surroundings. These are, as it were, conventional delusions established in infancy For, in fact, our sensations are the mere masks and symbols of reality, which is filtered through our sensory recording apparatus, but of whose true nature we can never have direct experience. The situation is very like that of a radar operator who can unfailingly detect a ship as a blob on his screen, without necessarily ever getting an idea of what it really looks like.

Finally, all sense organs obey certain physical laws. There is a minimum or threshold value for the stimulus, below which it is ineffective, and this level depends to some extent on physiological factors: it is higher in fatigue, or if there are simultaneous distracting stimuli. Further, we do not experience sensations in an intensity directly proportional to the true physical intensity of the stimulus; there is such an enormous range of impressions coming from the outside world that we have, as it were, to summarize them. Thus, a light which we feel to be twice as bright as another is, by physical measurement, perhaps ten times as intense, and this relation applies to sound also, i.e., it is a logarithmic one.

The Eye. The globe of the eye is a sphere of almost an inch in all diameters, with a more acutely convex bulge at the front formed by the transparent window of the cornea. The optic nerve is attached behind and runs back like a stalk into the cranial cavity. The eyeball has three coats:

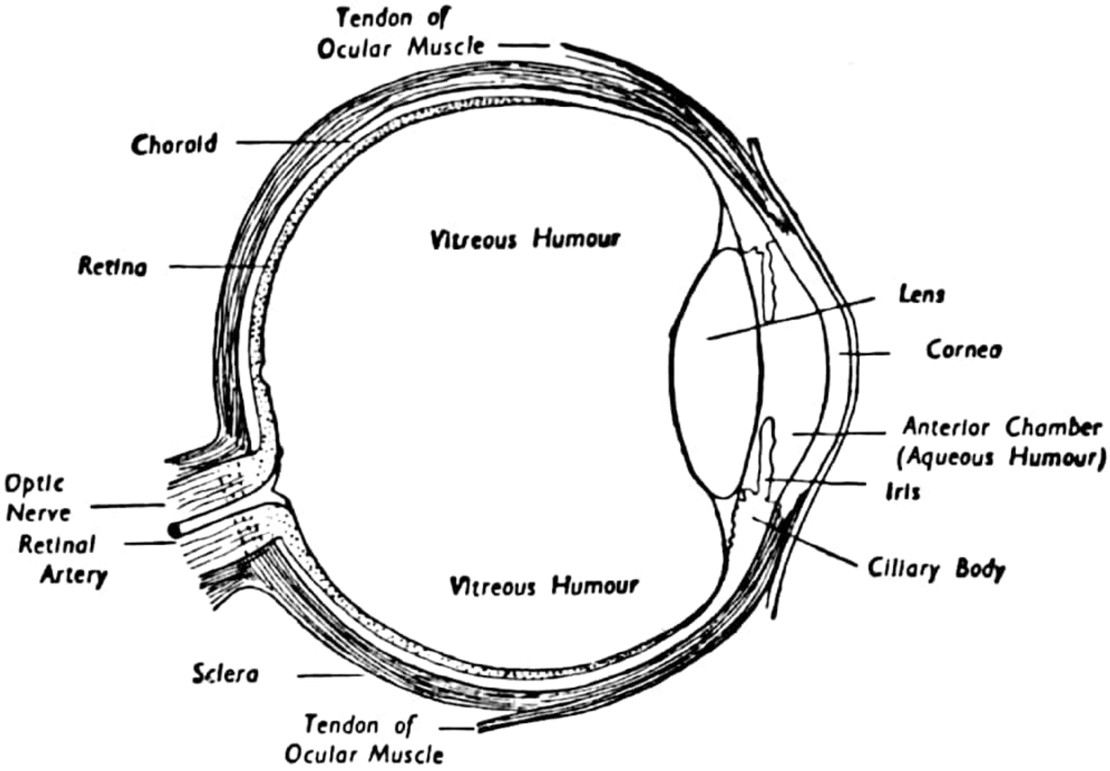

FIG. 30.—Section through the globe of the eye.

(1) The outer protective *sclera,* the opaque white of

the eye, surrounding the whole globe save where it merges into the *cornea* in front.

(ii) An intermediate pigmented layer, the *choroid*, lining the sclera ; it is this layer which is modified in front to form the *iris diaphragm* of variable aperture immediately in front of the lens, the opening of the pupil.

(iii) The internal nervous lining is the *retina*, adapted for the reception of light stimuli, a pigmented layered pattern of nerve cells, whose fibres exit in the optic nerve. Where the nerve is attached to the retina, there is no room for visual receptors, and this is consequently a blind spot.

The refracting media of the eye are also three in number :

(i) The watery *aqueous humour* fills the anterior chamber, the space between lens and cornea ; like the cerebrospinal fluid, it is being constantly secreted from the circulation and reabsorbed, and any accumulation leads to a dangerous rise of ocular tension, glaucoma.

(ii) The translucent solid *lens* can be modified in curvature so as to accommodate for near and far vision.

(iii) The bulk of the eye is filled with the thin jelly of the *vitreous humour.*

The eye as an optical system. We may compare the eye with a camera, much to the former's advantage. Focussing is automatic ; the lens changes its shape, or accommodates, so as to become more curved and powerful for near vision and less so for distant objects, the aim being always to bring the rays of light to convergence exactly on the retina and not in front or behind. The intensity of illumination of the retina is also adjusted automatically by the variable size of the pupil. There is a very wide field of vision, over 200° of a circle, so that objects slightly behind one's level are still in sight, and there is little loss of light by reflection at the refracting surfaces. The cup-shaped retina is everywhere in just the position for the best definition of the image,

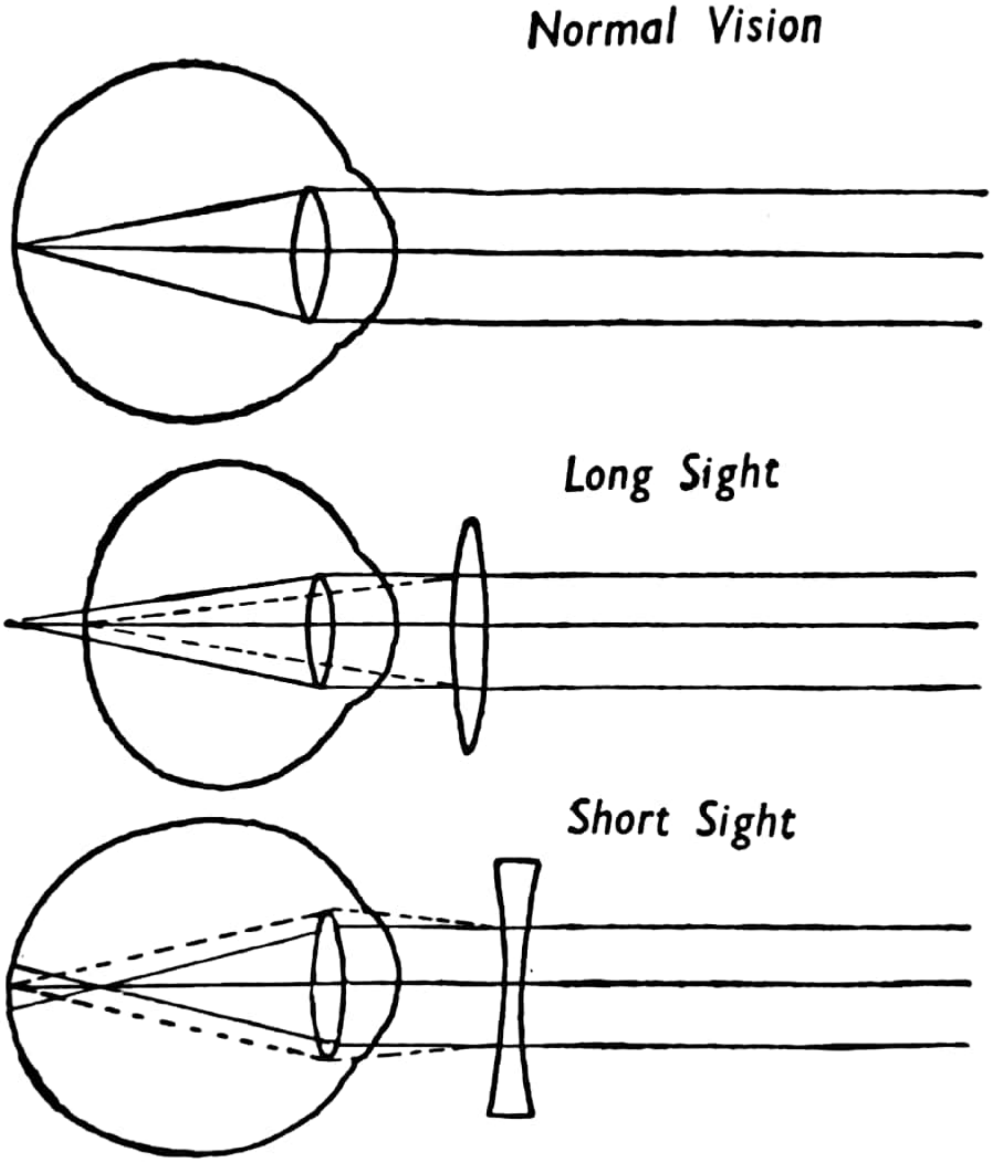

FIG. 31.—The focussing of parallel light rays by the optic lens in normal vision, and in long and short sight. When there is a refractive error an artificial lens has to be used to help make the rays converge on the retina, and the dotted lines show how this is achieved.

and it has two different systems of receptor cells. One set is for bright light and colour vision ; the other for blacks, whites and greys under twilight conditions. When the first system is defective, the individual is colour-blind, either partially for reds and greens, or completely so; in this case he must use his twilight apparatus for daylight purposes and all objects appear only different shades of grey. When the twilight apparatus is deficient there results the condition of night-blindness.

Longsightedness is normal in early childhood, for the eyeball is too small for proper convergence. If the condition persists in adults, light rays are converging behind the retina, and the condition is therefore corrected by the use of an additional artificial convex spectacle lens to supplement the converging power of the natural lens and focus the rays sharply on the retina. The long sight of old age is due to the degeneration and loss of resilience of the lens at this time, so that it cannot assume a more convex shape.

In shortsightedness, or *myopia*, rays are being focussed in front of the retina by too powerful refraction, and objects are blurred. This is corrected by using a supplementary concave lens of just sufficient power to displace the point of convergence backwards on to the retina.

It will be seen that errors of refraction in either direction may be due, not only to inadequacy of the lens system, but also to an eyeball which is too short or too long. The short eye and consequent long vision of infancy give place with growth to an eye of normal length and focussing capacity; but too much reading and close work cause the eyeball to go on increasing in size, and then the child becomes permanently myopic.

Binocular vision is important for several reasons. The combined use of both eyes gives a wider field of vision and eliminates the screening effects of nose and brow which shut off part of the field from a single eye. And it provides the stereoscopic effect, the appreciation of depth and distance ; this depends on the fact that the images of an object formed by each eye are slightly different, and that these two images are presented simultaneously to the brain without appearing double. Each eye, in other words, sees a little way round its own side of the object, and this information is fitted together in consciousness. To secure this, both eyes must converge on the focussed object, even though the angle of convergence is only slight for distant points. In many individuals with weak eye muscles and poor converging power, the single image is easily dissociated into two ; and if there is a habitual preference for using a better eye, the image of the weaker one is permanently suppressed, so that this eye may become virtually blind. The flatness of vision of the one-eyed man is notorious ; but it is not complete. He gets a fair idea of depth from shadow contrast, surface reflections, and the modifying effect of distance on colour.

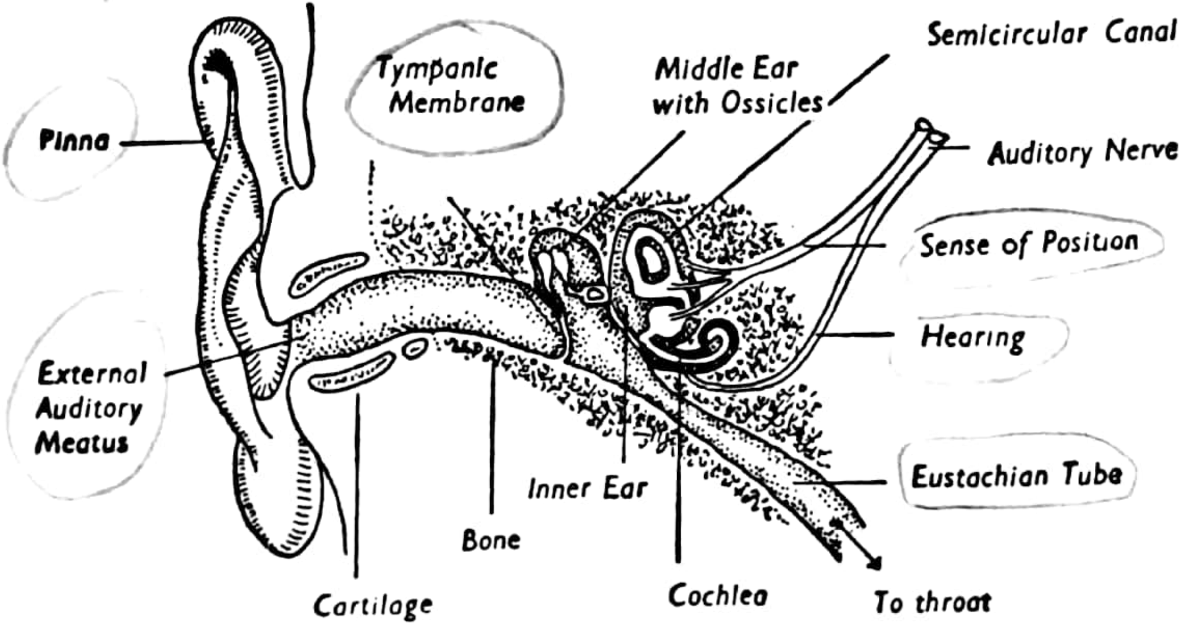

FIG. 32.—The ear.

The Ear. This organ falls anatomically into three parts (Fig. 32). These are, from without inwards :

(i) The *external ear,* the obvious funnel for the collection of sound waves, which leads along a narrow channel into the skull. At the bottom of this passage the eardrum or *tympanic membrane* forms a tense partition between the outer and middle ear cavities.

(ii) The *middle ear*, a small cavity beneath the base of the skull spanned by three tiny bones, the *auditory ossicles*, which link the tympanic membrane with the wall of the inner ear. These ossicles transmit by cone conduction the vibrations set up by sounds in the resonant eardrum.

(iii) The *internal ear* or labyrinth, a complex organ deep in the skull. Its upper part is concerned only with appreciation of position and orientation, and consists of three fluid-filled *semicircular canals*, arranged mutually at right angles in the three planes of space. Change in posture causes movement of the contained fluid, which excites the hair-cells lining the canals, and these impulses are transmitted in one portion of the eighth cranial nerve (Fig. 33).

The lower part of the labyrinth is the *cochlea*, the true organ of hearing, a spirally coiled structure responding to sound and transmitting impulses of different pitch through the acoustic portion of the eighth nerve. These impulses enter consciousness, whereas those of position sense go to the cerebellum, which automatically adjusts body posture in response.

The tension of the eardrum is not constant, but is adjusted by a special muscle, which relaxes when no sound is to be heard. The membrane responds very faithfully to high and low notes of frequencies ranging between 40 and 30,000 a second, and transmits these vibrations to the chain of ossicles in the middle ear; these in their turn beat against the bony case of the labyrinth and stimulate the cochlea. The middle ear cavity is connected with the throat, and thus with the outer atmosphere, by a narrow canal, the Eustachian tube (Fig. 32), which is normally closed; its function is to keep the air pressures identical on both sides of the drum. If the atmospheric pressure is suddenly altered, as in an aeroplane ascent, or in a sudden change of level in a tube train, there is temporary deafness, until the canal is opened by yawning or swallowing, when equalization is restored.

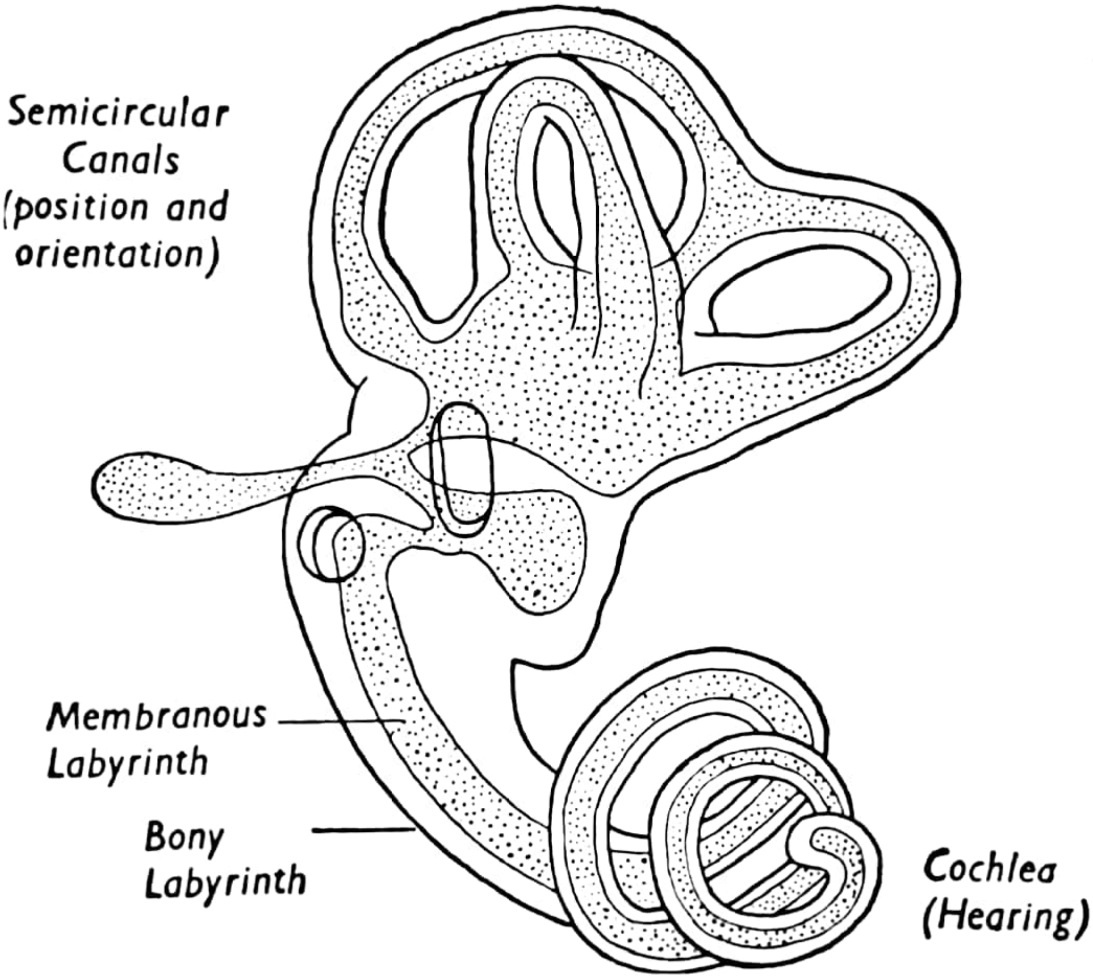

Fig. 33.—Internal ear.

The Nose. The sense of smell is vestigial in man, varying greatly from one individual to another; nevertheless it remains one of the most delicate of all the senses. It depends on odoriferous particles actually reaching the nose and there dissolving in the moisture of the mucous membrane. The actual sensory area is a particular patch of membrane situated at the very summit of the nasal cavities and rather out of the way of direct air-currents through the nose. There is therefore a little delay before a new odour is appreciated while the particles diffuse upwards. And it must be recalled that violent and pungent " smells ", like those of ammonia, are really stimuli of ordinary sensation within the nose and are transmitted by a different nerve.

Taste, like smell, is a chemical sense and depends on the entry of foreign particles into solution on the surface of tongue and palate, a sampling process to decide the question of rejection or acceptance. Special microscopic organs or *taste buds*, embedded in the mucous membrane, serve this function, and in the tongue these

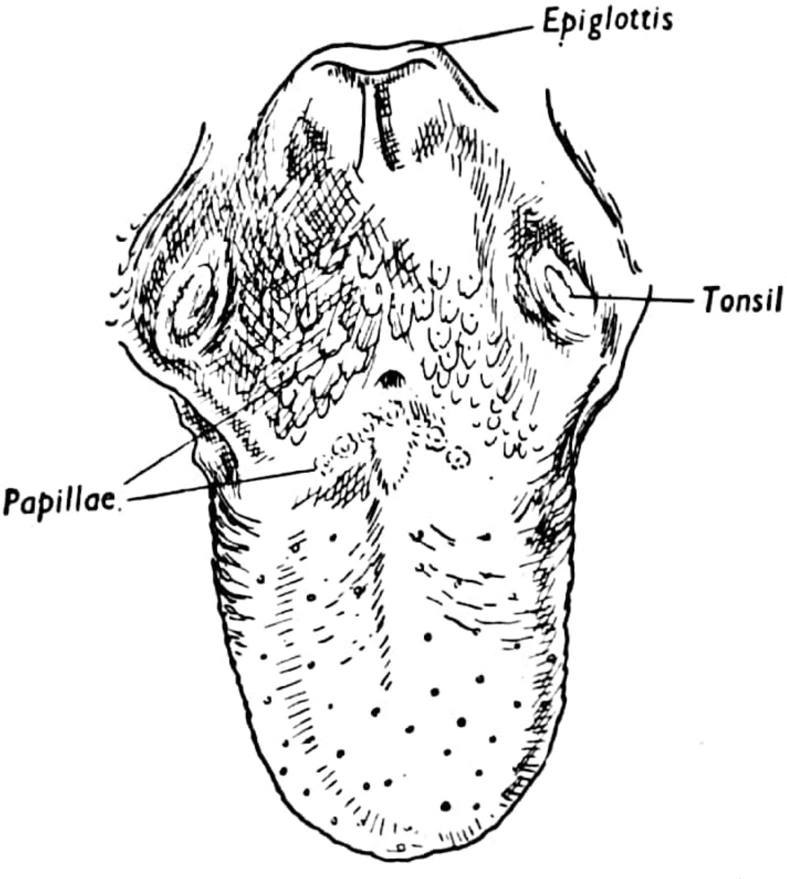

FIG. 34.—The upper surface of the tongue, showing the papillae on which are grouped the taste buds.

are grouped into obvious projections or *papillae*. There are four basic tastes—sweet, sour, salt and bitter ; and these, when mixed, do not blend, but remain distinguishable. The nature of any taste depends on the chemical composition of the substance concerned and particularly on its acidity or alkalinity ; and different parts of the tongue tend to "specialize" in different tastes. We have already noted that many so-called tastes and flavours are really smells, and are lost when the latter sense is put out of action ; food and tobacco are savourless during a severe cold.

The Skin as Sense Organ

The skin is the bounding layer which intervenes between the body and the outside world, so that its sensory reactions to stimulation are of the first importance. In fact, the special sense organs of eye and ear, and the central nervous system itself, have developed in evolution, and also in the embryonic history of the individual, from an infolding of this surface layer. The sense of *touch* is transmitted by small organs or end-bulbs of the cutaneous nerves, lying in little bays on the deep surface of the epidermis (Fig. 35) ; and touch is essentially a response to distortion of the skin surface, not to mere pressure, for the skin soon becomes adapted to, and ourselves unconscious of, the continuous pressure of clothes. The hairs play an important part by acting as levers magnifying the effects of a contact, and the sensory bulbs are grouped around their roots in profusion ; hence the phenomenon of *tickle*, and the general blunting of sensation which follows the shaving of a hairy surface. Touch sensibility is not uniformly distributed, but is scattered in a number of *touch spots*, separated by about half a millimetre, and between these there is no sensation. The capacity of discriminating between two adjacent stimuli varies from place to place ; on the tongue and fingertips two compass points are felt to be separate if only $\frac{1}{25}$ of an inch apart, but they must be separated $2\frac{1}{2}$ inches on the thigh before being appreciated as distinct.

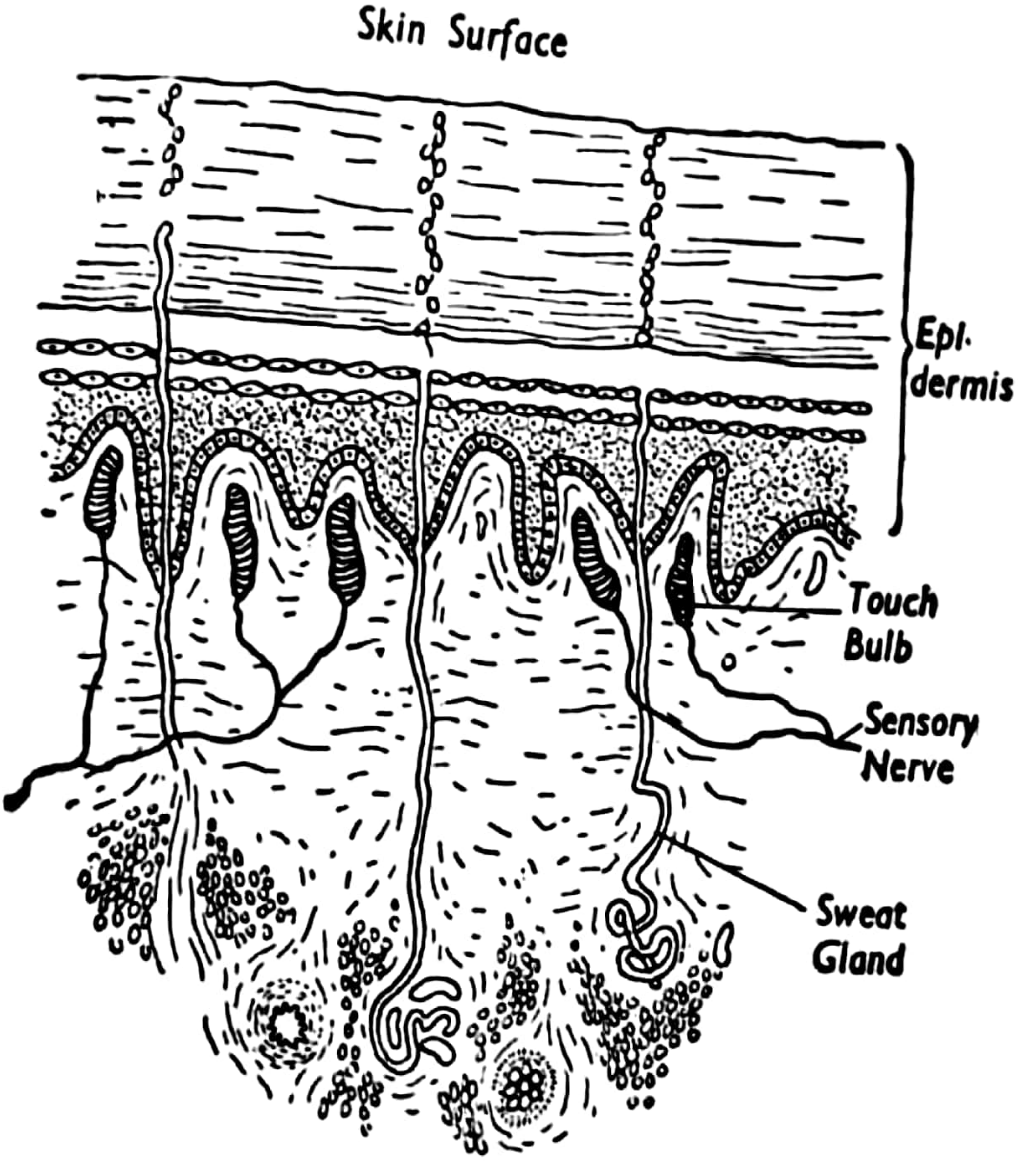

Fig. 35.—Section of the skin showing touch bulbs and sweat glands.

The skin offers a good instance of how our conventional reading of sensations depends merely on habituation. A pencil point slid between the tips of the middle and index fingers is felt as one stimulus because these surfaces are normally adjacent and we have learnt to fuse their sensations ; but, if the fingers are crossed surfaces which are never normally in contact are brought together and a pencil placed between is now felt as double.

Pain sense is due to an increase of pressure above the maximum threshold for touch sensation, but it is appreciated by a different set of skin organs, distributed in pain spots which are not identical with the touch spots. The two are usually so intermingled that exact differentiation is difficult, but the cornea of the eye is an instance where *any* stimulus is felt as pain and there is no ordinary touch sensation. The object of pain sensation is to protect the individual from danger by provoking an automatic withdrawal reflex, and such a response still persists in animals whose brains have been destroyed, and in men suffering from paralysis due to loss of the connections between brain and spinal cord. When pain sense is lost in nervous disease, the sufferer may burn himself and remain unaware, and the skin becomes particularly liable to ulceration and rapid infection.

Temperature Sensation. Feelings of heat and cold are due to a loss or gain of heat from the object felt. The importance of this gradient is shown by the familiar trick of chilling one hand and overheating the other, when tepid water is felt as hot by the one and cold by the other. As with touch, temperature sensation is distributed not uniformly but in discrete points of the skin surface, and there are separate sets of receptors for the two kinds of stimulus—the heat and cold spots. The mucous membranes are less sensitive to heat than the exposed parts, so that one can drink fluids which are too hot to be poured on the hand. It is a matter of common observation that there is a qualitative difference between the hot and the merely warm ; very hot water often feels cold for a time and this may be due to a *total* stimulation of all the temperature end-organs. But the problem of temperature sense is complicated by the changes which stimuli produce in the small blood vessels of the skin ; if these open up, the part becomes warm because flushed with blood, while constriction results in pallor and coldness. Thus a painful stimulus often causes vasodilatation and hence is spoken of as a burning pain, because heat and pain receptors are being simultaneously excited.

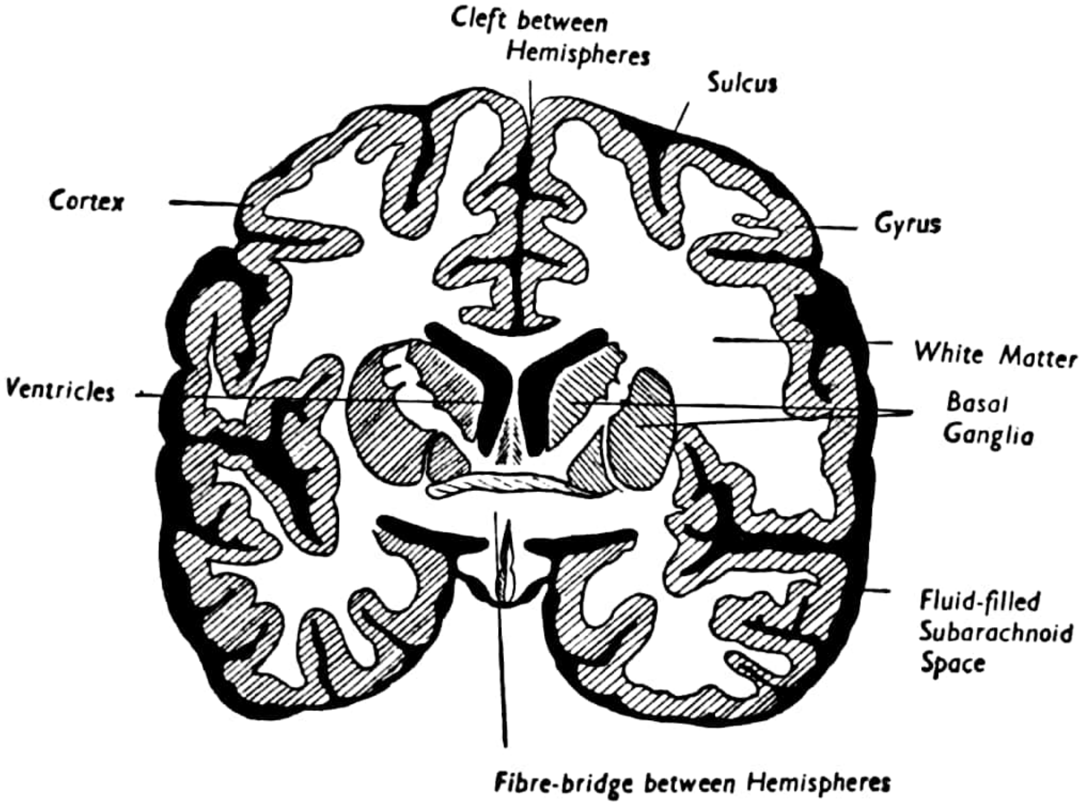
Cleft between Hemispheres
Sulcus
Cortex
Gyrus
White Matter
Ventricles
Basal Ganglia
Fluid-filled Subarachnoid Space
Fibre-bridge between Hemispheres

FIG. 36.—The forebrain in cross-section.

CHAPTER XIII

ENDOCRINE GLANDS

There has always existed in the animal kingdom a duality in the methods of responding to stimulation. The most primitive method is by an alteration of the chemical substance of the protoplasm at the stimulated point, with the diffusion of the chemical agent to other parts of the body, where it excites a general reaction. The more sophisticated method is the development in evolution of a nervous system, with ramifying communications and a central control for incoming and outgoing messages.

But the primitive chemical mechanism has been retained, and even developed, in the higher animals. The *endocrine* system is a group of glands, without obvious ducts; their secretions are internal, i.e., they are absorbed into the blood-stream and diffused throughout the body, on whose functions they exert an intimate and profound control. These secretions are the *hormones*, or chemical messengers; and these glands obviously differ entirely from the glands of external excretion, like the liver and salivary glands, which have ducts carrying their juices into a body cavity or on to the skin surface. Nevertheless, some organs are capable at one and the same time of both internal and external secretion; the pancreas secretes digestive juice into the bowel, as well as insulin into the blood, the ovaries and testicles form ova and spermatozoa as well as the male and female hormones.

A general characteristic of hormones is the extreme

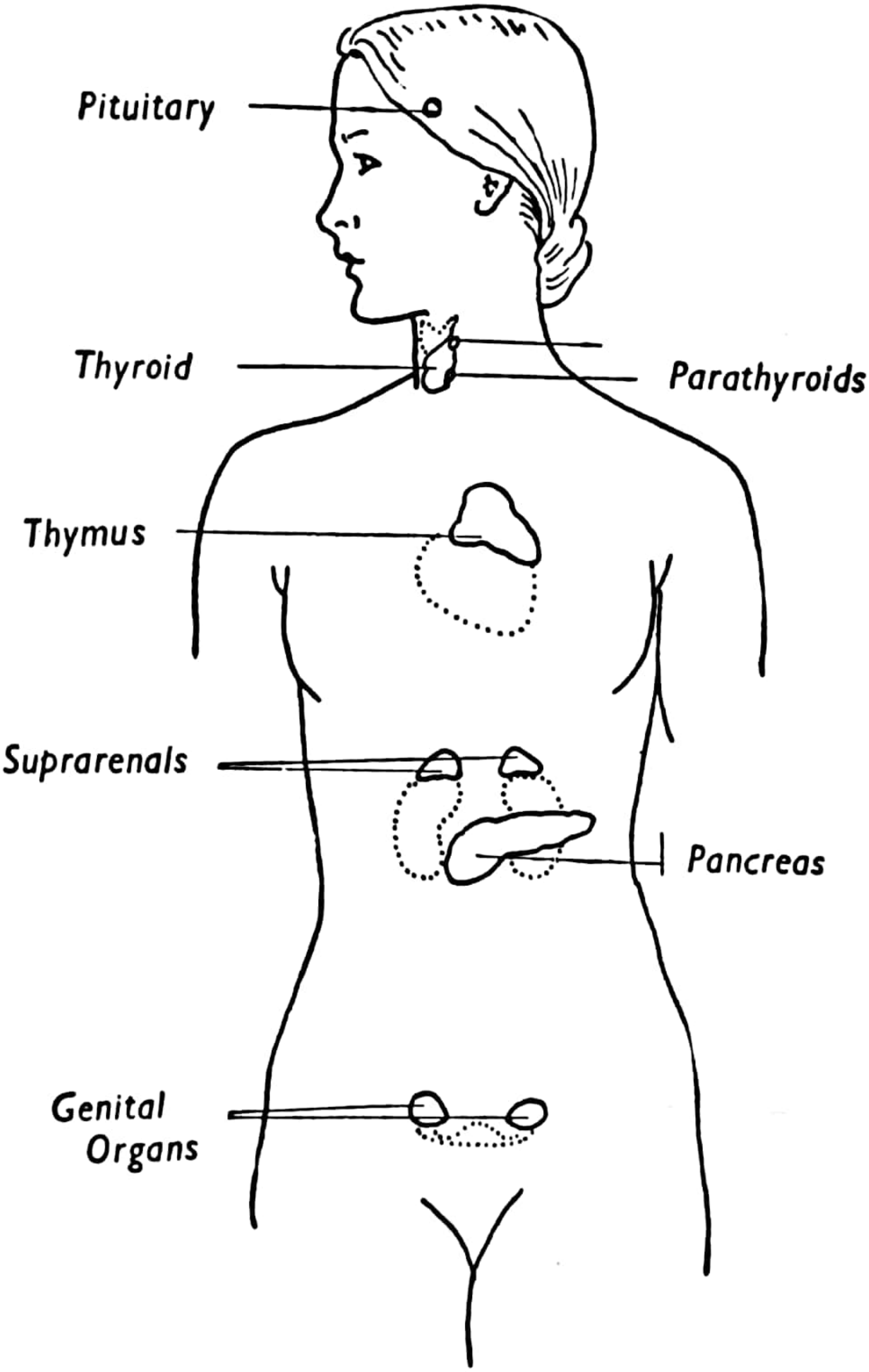

FIG. 37.—The endocrine glands.

potency of even minute amounts of the secretion. We may recognize three main types of endocrine activity :

(i) A *temporary response* to meet the needs of an emergency, e.g., the liberation of adrenaline from the adrenal glands in alarm.

(ii) A *sustained activity*, e.g., the constant stimulating action of the thyroid gland on metabolism.

(iii) The secretion of the *sex hormones* by the male and female sex organs.

All these activities are concerned with the basic processes of the body, and are not independent of nervous control, for they are affected by the autonomic nervous system and subject to emotional influences acting through this system. And all the endocrine glands are closely interrelated and affect each other's activity ; the precise nature of this balance in the individual is a large factor in the determination of personality. They have been compared to an orchestra, of which the leader is the pituitary gland.

The **Pituitary gland,** a pea-like organ slung from the under-surface of the fore-brain, occupies a little socket in the base of the skull. Though not essential to life, disease or removal of the whole gland results in arrest of growth, atrophy of the sexual organs, general weakness, and premature senility. It consists of two lobes, each of which produces several types of hormone.

Front lobe. This is concerned with growth, particularly of the skeleton ; in childhood any over-action leads to gigantism, any deficiency to stunting or dwarfing. In adults, the effects of over-activity are less dramatic, for the epiphyseal ends of the long bones are closed (p. 20) and extreme growth in height cannot occur ; but in its place there develops the condition of *acromegaly*, an enlargement of the head and hands accompanied by some mental retardation, producing an individual of the Carnera type. The front lobe is also intimately related to sexual activity. In the female it controls the cycle of menstruation, the development of the ova, the growth of the pregnant uterus, and has something to do with the processes of childbirth and the secretion of the mother's milk. In the male, it is responsible for the development of the testicles in the abdominal cavity and their descent just before birth into the scrotum.

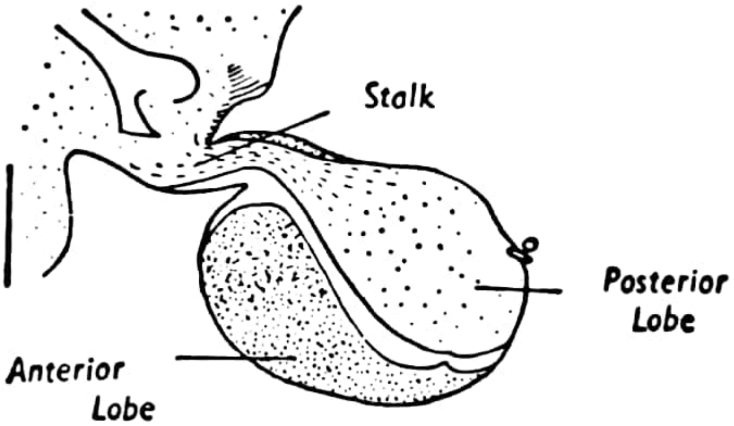

FIG. 38.—The pituitary gland, longitudinal section. (After *Gray*.)

Back lobe. This again has several actions. It helps to regulate the water-balance of the body, and any disease causes the passage of excessive quantities of pale dilute urine. It also increases the tone of involuntary muscle generally ; thus it raises the blood-pressure by constricting the small vessels, and helps to empty the bowels and bladder and the uterus (womb).

The pituitary has a particularly close and reciprocal relation with the next gland on the list.

The **Thyroid** gland is situated in the lower part of the neck, as a large lobe on either side of the wind-pipe. Its secretion is *thyroxine*, which stimulates the rate of metabolism—the cycle of building-up and breaking-down processes—as a bellows keeps a fire going. Any excess of secretion causes marked overexcitability and nervousness, a rapid pulse, staring eyes and an appearance of alarm, with general wasting, i.e., the condition known as *Graves' disease.* Deficiency in adult life causes an obese slow-wittedness, with falling out of the hair, and slowing of both mental and physical performance ; but deficiency in childhood stops the growth of the skeleton and produces the *cretin*, an ugly, stunted, pot-bellied and mentally deficient individual with a protruding tongue. Such deficiency may be due to congenital absence of the gland, or may be the sequel to a low incidence in the soil and water of the district of iodine, which is an essential constituent of thyroxine. Such an iodine deficiency is the cause of goitre, a bulky enlargement of the gland which struggles vainly to make up in quantity what it has lost in quality. Fortunately, the ill effects of thyroid lack can be entirely compensated by feeding with thyroid extract ; and when the condition, as in Switzerland, is due to iodine deficiency, the iodization of table salt is quite adequate to prevent symptoms.

The **Parathyroid** glands are four tiny structures embedded in the thyroid capsule. They control the metabolism of calcium, and hence the degree of calcification of the skeleton. An overactive tumour of these organs transfers calcium in great quantity from the bones to the blood-stream, from which it is excreted in the urine ; the bones become rarefied and brittle and fracture easily.

The **Adrenal** glands are found in the abdomen, two in number, each perched like a small cap of liberty on the upper pole of its corresponding kidney. Like the pituitary, the adrenal is of complex structure and multiple function. It has an inner core, or *medulla*, which is intimately connected with the sympathetic nervous system and has, in fact, developed in common with it.

Through its hormone—*adrenaline*—the same effects are produced in response to an emergency as follow a sudden flaring up of sympathetic activity in the autonomic system. There is a speeding-up of the circulation and a rise in blood-pressure; glycogen is mobilized from the liver and poured as sugar into the blood, the eyes stare and the hair stands on end. In other words, the adrenal, like the sympathetic with which it acts in conjunction, responds to a threatening situation by preparing for fight or flight. However, this medullary function is not essential to life—unlike that of the outer rind or *cortex* of the gland. This controls the metabolism of water and salt throughout the tissues, and gross deficiency results in increasing weakness and prostration with profound lowering of the blood-pressure and eventual death. It also has a close connection with the sex glands. It is difficult to say exactly what this connection is under normal circumstances, but some hint is given by the fact that abnormal function of the adrenal cortex can either bring on precocious sexual development in boys and girls, or it can actually tend to *reverse* the sexual characteristics, producing masculinity in women and feminism in men. Such a reversal does not, of course, alter the essential nature of the sexual organs of the individual, but changes the external appearances, such as the growth of hair and the body contour, as well as the psychological make-up and the direction of sexual desire. Many unfortunate women looking like men, and with male sexual desires, are the victims of an overacting tumour of the adrenal cortex, and some have been cured by its surgical removal.

The Gonads or Sex Organs. The ovaries and testicles, besides their prime function of forming the reproductive cells—ova and spermatozoa—secrete the female and male sex hormones respectively. These are responsible for the development of what are known as the *secondary sexual characteristics*, the attributes, though not the essentials, of male and female sexuality. These include hairiness, deep voice, coarse skin, the pubertic enlargement of the external genital organs, and a narrow pelvis, in men; hairlessness, smooth skin with plenty of subcutaneous fat, the development of the breasts, and the broad pelvis of women. And they also include the less definable but important differences in male and female personalities and attitudes.

The **Pancreas** has, as its internal secretion, *insulin*, to which we have already referred fully in Chapter VI, p. 75; its function is to ensure the proper utilization of sugar by the tissues, and its deficiency is the cause of diabetes.

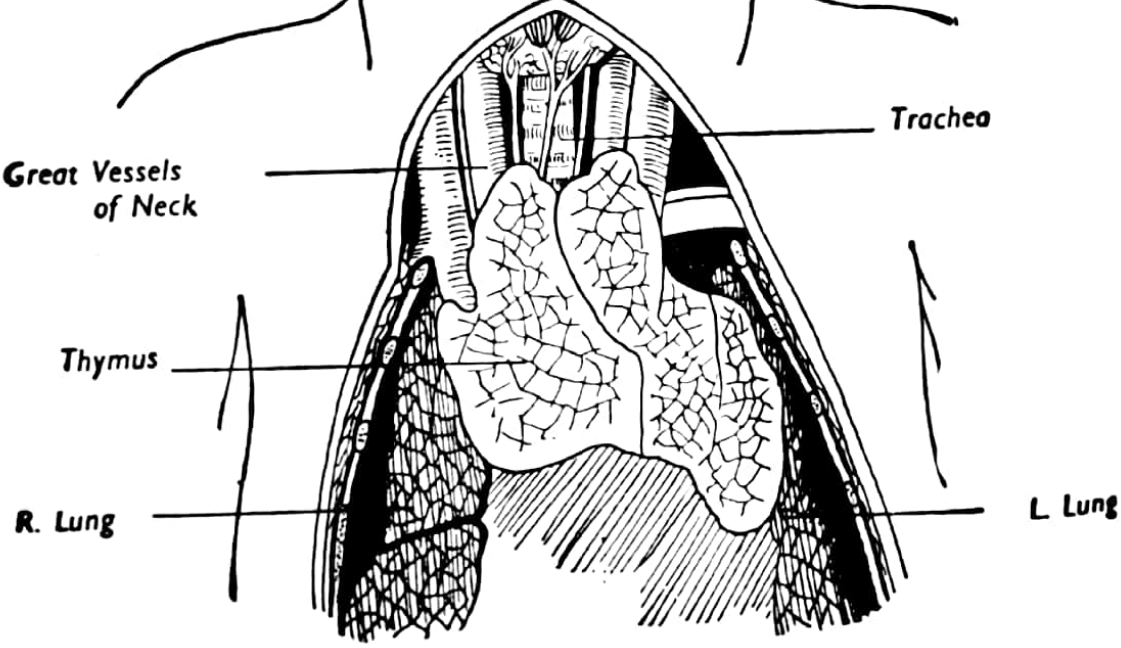

FIG. 39.—The thymus in the new-born child. (After *Gray*.)

Two other organs are sometimes classified as endocrine glands, though it is by no means certain that they possess any specific function. The *pineal* organ is a tiny outgrowth from the roof of the brain, a vestigial relic of the third eye at the top of the skull possessed by certain lizards. The *thymus* is a large lobed gland, found behind the breastbone in the newly-born child (Fig. 39). This gland rapidly atrophies and disappears after the first few years of life. It has been thought that a persistent thymus might be associated with a tendency to sudden death under anaesthesia, but little evidence exists to support this. Much more important, it has recently been shown that a serious lingering and ultimately fatal disease, characterized by marked weakness of every muscle, and known as *myasthenia gravis*, can be dramatically cured in many instances by surgical removal of the thymus gland.

CHAPTER XIV

REPRODUCTION

THE essential sex organs are known as the *gonads*—a pair of *testes* in the male, forming the male germ cells or *spermatozoa*, and a pair of *ovaries* in the female, forming the egg-cells or *ova*. The general plan of the reproductive system in both sexes is not dissimilar in development, though the final adult forms appear, and are, very different, owing to the suppression and over-growth of particular organs. Thus, while the ovaries remain within the abdominal cavity, the testes come to lie outside it ; there is a womb or uterus in the female for housing the developing embryo, which has no equivalent in the male ; and the masculine penis is represented in the woman only by the diminutive equivalent structure called the clitoris.

In animals, reproductive activity and sexual desire is usually an intermittent affair, periods of sexual desire alternating with seasons of indifference ; even when the male is continuously active, the female tends to be receptive only in cycles, dependent on a recurring rhythm of activity in the ovaries ; and the formation of the sex hormones is correspondingly discontinuous. In man, the pressure of sexual feeling is pretty constant, particularly in the male, and the secretion of the sex hormones is on the same level. There is still some periodicity in the female, associated with the monthly phenomenon of *menstruation*, a flow of blood and mucus from the womb which only occurs in the higher apes and man.

We have already seen that the development of the sexual organs before puberty, and their proper functioning thereafter, is dependent on the pituitary gland. This influences the enlargement of the organs in childhood, and is responsible at puberty for their beginning to function ; but when this time arrives it is the hormones of the sex organs themselves which cause the development of the secondary sexual characteristics, which impart the outward forms of masculinity and femininity—in both sexes the origin of sexual desire, in the girl the swelling of the breasts and the commencement of menstruation, and in the boy the change of voice and enlargement of the external organs. All these changes are dependent on the primary development of the ovaries and testes and will be prevented if these organs are ineffective because of disease or castration.

Male Organs. Man is peculiar among mammals in that the testes develop in the abdominal cavity, but pass down shortly before birth to enter the loose skin pocket of the *scrotum* externally, where they hang down on each side of the root of the penis. But a passage through the abdominal wall above the groin on either side still transmits the stalk of the organ, and carries the sperm duct back to the abdominal cavity.

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The *testes* are rounded structures, in which the microscopic spermatozoa are being continuously formed within fine tubules ; it is because this process of sperm formation is slowed down or stopped by excessive warmth that the testes make their original descent, and a retained abdominal organ rarely functions. The sperm pass out into a curved organ, the *epididymis*, applied to the outer side of the testis, and from this the main spermatic channel or *vas deferens* runs up to the abdomen. Here it empties the sperm into a storage receptacle or *seminal vesicle.* The two vesicles lie at the back of the bladder, above the prostate gland ; in the final ejaculatory act of sexual orgasm, they discharge their sperm into the channel or *urethra* which normally carries the urine ; this emerges from the base of the bladder to traverse the prostate, pierce the pelvic floor, and enter the penis, opening at its tip.

The *penis* consists of three bundles of tissue bound together, one of which conducts the urethra. This tissue is pervaded by a system of cavernous spaces, which can be rapidly distended with blood from the penile arteries ; and it is to this that the organ owes its remarkable property of *erection* from the flaccid state, an increase of length and girth in sexual excitement, making it rigid and capable of introduction into the female vagina, where the sperm are deposited. It should be noted that the ejaculate is not simply the spermatozoa, but a complex *seminal fluid* including the secretions of vesicles and prostate.

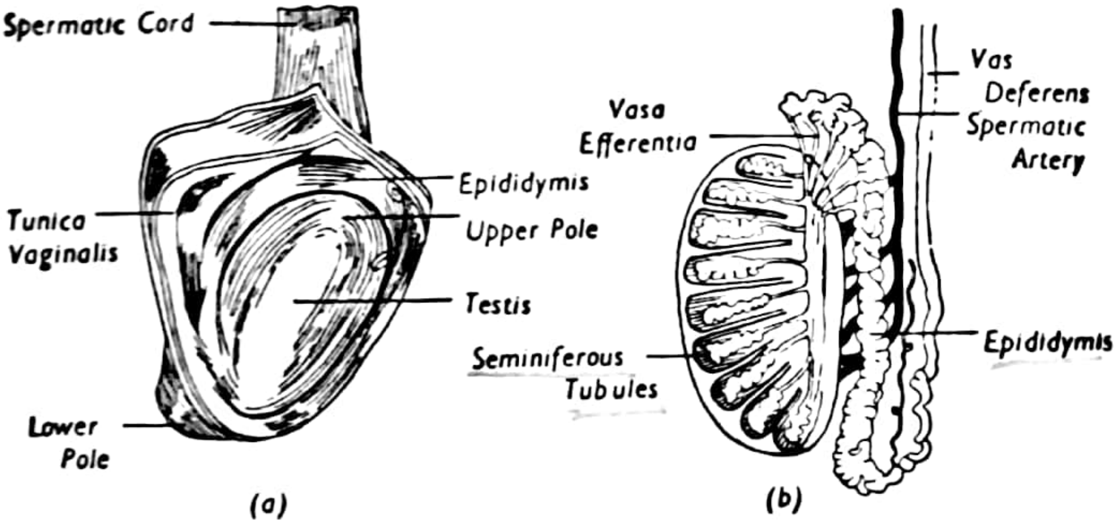

FIG. 40.

(*a*) Testis and epididymis exposed by reflection of their serous covering, the tunica vaginalis.

(*b*) The same in longitudinal section.

Female Organs. The *ovaries* are a pair of almond-shaped organs, lying one on each side of the pelvic cavity; they are studded with fluid-filled cysts, the *ovarian follicles*, in which the ova ripen, one coming to maturity every month. Each ovary discharges its ova into a muscular channel, the *uterine tube*, and the two tubes empty into the uterus.

The *uterus* or womb is a hollow structure, with powerful muscular walls, lying in the centre of the pelvis, between the bladder in front and the rectum behind, and communicating with the vagina below. A section through it shows the main upper part or *body* and the narrower *cervix* below, protruding into the *vagina*. The vagina is a distensible canal, capable of receiving the penis during sexual intercourse, and of allowing the passage of the child during parturition. It runs from the uterus through the pelvic floor to open externally. The external female organs are known collectively as the *vulva*. Greater and lesser lips or *labia* surround the opening of the vagina, which is partly closed in the virgin by the partition of the *hymen*; and the *clitoris* represents the diminutive female equivalent of the male penis. The urethra opens between clitoris and vagina.

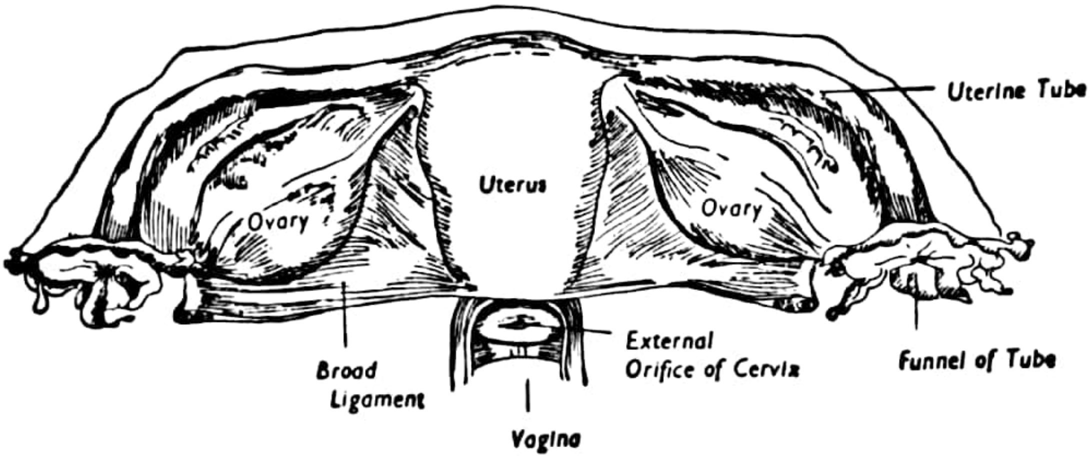

FIG. 41.—The internal sex organs of the female.

We may now give a brief account of the reproductive process. Each month an ovarian follicle ripens in the ovary, discharging an ovum which is taken up by the uterine tube and propelled by muscular contractions of this tube towards the uterus. Here the lining membrane has become highly vascular and thickened in preparation for the possibility of the embedding of a fertilized egg; and if, as is usually the case, fertilization has not taken place the uterine lining is eventually shed to cause the bleeding of menstruation. This is taken as the beginning of the monthly menstrual cycle; it lasts 3–5 days and then a new lining begins to be built up again and is completed by the fourteenth day of the cycle, midway between two periods; and it is precisely at this time that ovulation occurs again in the ovaries. Thus the cycle affects both ovaries and uterus, ovulation and menstruating alternating regularly at fortnightly intervals; the uterine lining waits built-up and receptive during the latter half of the cycle, it is destroyed at menstruation if

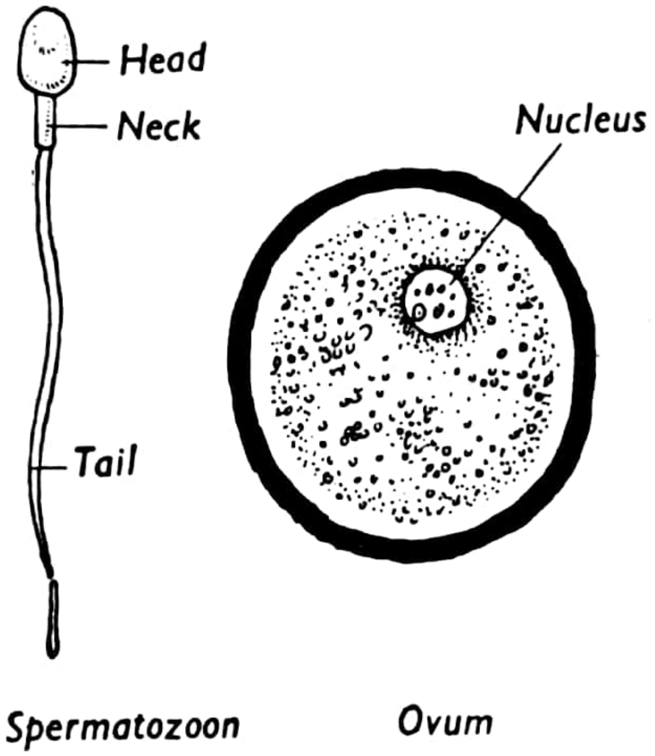

FIG. 42.—Male and female reproductive cells.

conception has not occurred, and it is rebuilt again in the first half of the next cycle.

Fertilization, the union of the male spermatozoon with the female ovum, takes place within the uterine tube as the egg is moving towards the uterus. It can only occur if, at this precise time, a living sperm derived from the male by recent intercourse has made its way up the vagina, through the cervix and body of the uterus, and into the uterine tube ; success, therefore, depends on a near coincidence of intercourse and ovulation within about 48 hours ; and the likelihood of any single sexual act resulting in pregnancy is therefore a small one.

Sterility means the inability of a woman to conceive, i.e., to house a developing embryo within her uterus, but it is by no means a purely female problem. For when we survey the long line of processes necessary in both sexes for the proper development of the germ cells and their fusion, it can be seen that an error at any point in either sex may be responsible. Thus the sex organs themselves may be abnormal, diseased or absent ; the sperm may be few, malformed or non-viable ; the vaginal secretion may be lethal to them ; the uterine tubes may be blocked and prevent the passage of the ova. And we have seen that deficiency of vitamin E causes death of the very young embryo. Thus no investigation of sterility is complete until both parties have been examined.

Development of the Embryo. When the nuclei of the two germ cells have fused, the egg at once begins to divide or segment, and forms a rounded cell mass whose cell content is doubled at each division. This process begins before entry into the uterus, as the journey along the uterine tube takes several days ; once within the womb, the ovum adheres like a parasite, excavating for itself a cavity in the mucous membrane, where it becomes embedded and sealed off with blood clot.

The early embryo consists of little more than a pair of bubbles or vesicles, the *amniotic cavity* and the *yolk-sac*, with an intervening plate which is the actual *embryonic area* at which individual development occurs (Fig. 43). The amniotic cavity soon expands enormously, fills the whole uterus, and is occupied by the amniotic fluid in which the embryo floats during its growth within the womb. At the actual site of implantation in the wall of the uterus, the amniotic membrane develops a complex system of fringed vascular processes, which burrow into the uterine wall and interlace with the blood sinuses of the wall. This arrangement forms the mass of the *placenta*, a fleshy disc some 8 inches across at its greatest development, where the circulations of mother and child are in the closest proximity; but there is no direct communication between the two, and oxygen and food substances have to diffuse across the barrier. The second embryonic cavity, the yolk-sac, is soon squeezed by the

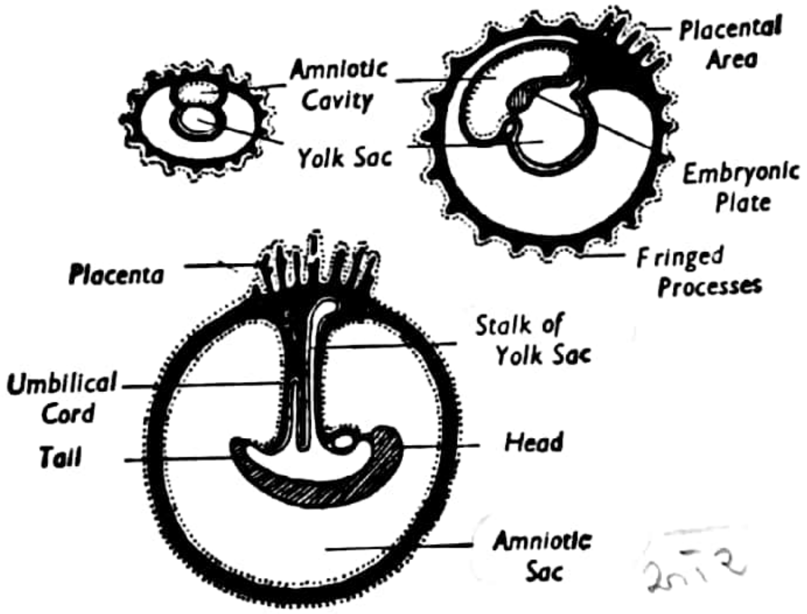

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FIG. 43.—Stages in the development of the early embryo.

growth of the amnion into a narrow stalk, the core of the *umbilical cord* which connects the child with the centre of the placenta (Fig. 44). This cord is 20 inches long at birth, is spirally twisted, and carries in its jelly-like substance the two umbilical arteries and single umbilical vein of the foetus. Since the foetus sends its stale blood to the placenta for oxygenation and nutriment, these blood vessels are analogous to the pulmonary vessels of the adult ; i.e., the arteries contain venous blood, the vein fresh arterial blood.

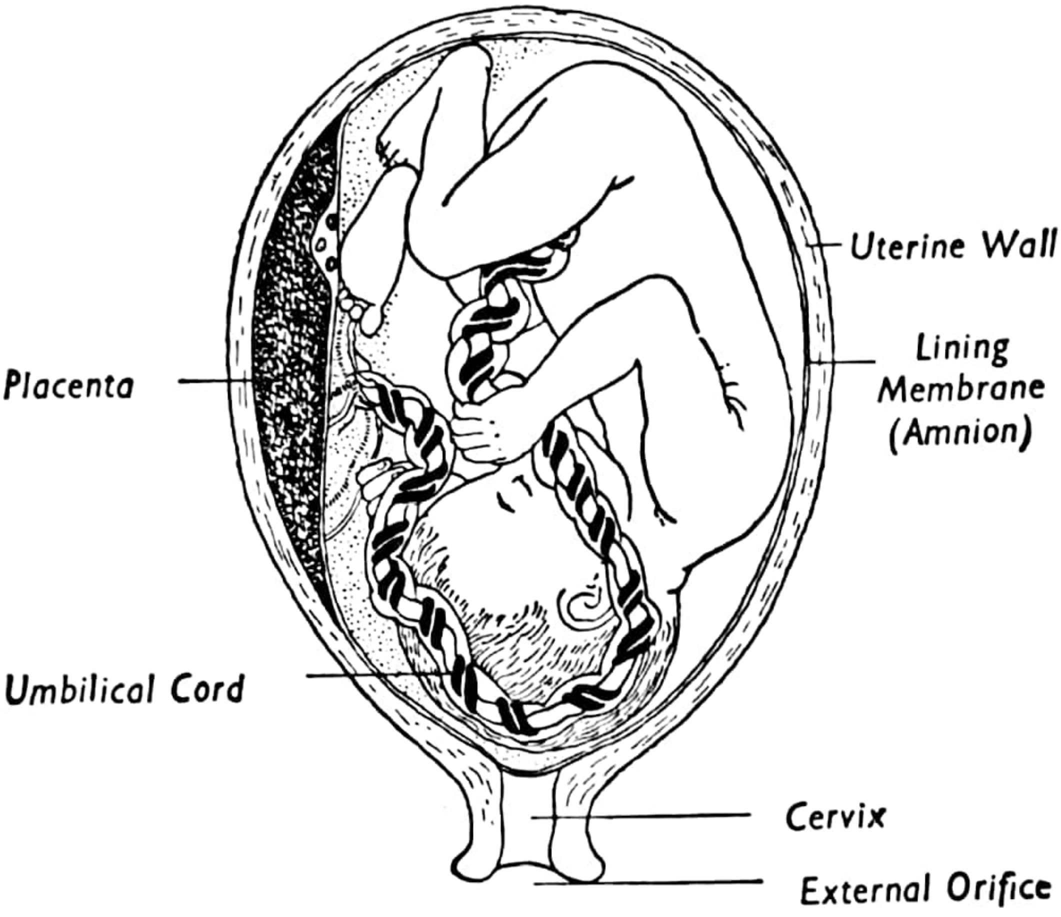

FIG. 44.—The foetus *in utero*. (After *Gray*.)

Embryonic Layers. The early embryo comes to possess three layers of cells from which develop all the body tissues and organs. The outermost layer or *ectoderm* forms the skin, with its associated glands, hair and nails ; the nervous system ; and the essential parts of eye, ear and nose. The nervous system originally lies on the surface at the back of the body, and is unfolded in development to become a tube which is the precursor of the spinal cord, with a bulbous expansion at the head end to mark the site of the brain. All the sense organs originate in this outer layer, an infolding of greatly modified skin surface meeting an outgrowth from the central nervous system ; this arrangement is well shown in the eye, where the retina, an extension from the brain on the optic nerve stalk, cups the transparent lens which has developed from the overlying skin.

The innermost layer or *endoderm* forms the whole of the bowel and associated glands, such as liver and pancreas ; the lining of the respiratory tract and lungs ; the thyroid and parathyroid glands.

The intermediate layer is the *mesoderm*, origin of all the connective tissues of the body ; the bone and cartilage of the skeleton ; the teeth ; all muscles of every kind ; the heart and vessels ; and the urinary and reproductive systems. The general features of the development of the limb buds and the ossification of the skeleton have already been outlined on p. 21.

At any point in this unimaginably complex pattern of development, things may go wrong, or may not go far enough. The spinal cord may be left on the surface of the body, as an open layer instead of a tube ; or it may develop normally, but the two halves of the spinal column may fail to enclose it properly. The palate may remain cleft, if its two halves fail to come together in the roof of the mouth ; the cardiac septum between the right and left halves of the heart may remain incomplete, allowing a vicious and disabling mixture of venous and arterial blood ; a bone or a limb may fail to appear, fingers and thumbs may be too few or too many. What is remarkable in all this is the overwhelming frequency with which the developmental process makes its way to an accurate ending at a constant time, reciprocal organs maturing together, and that any error is a rarity.

It may be useful to give a note on the times of certain important stages.

The two primitive vesicles of the *embryo* are present some 10 days after fertilization, and the intervening embryonic plate begins to develop to the third week ; head and tail folds, spinal cord and heart are obvious by the fourth week. In the fifth week appear the lens of the eye, the rudiments of the face, the gill arches (rudiments which are later lost), and the stumps of the limb buds ; and the embryo is now $\frac{1}{5}$ inch long. The sixth week sees the body well curved on itself, the head approximating to the tail ; the umbilical cord is attached to the belly near the tail end, the liver enlarges, and the limb buds grow out and are demarcated into their future segments.

By the end of the eighth week the embryo is an inch long and is thenceforward known as a *foetus* ; eyes, ears and nostrils are formed, the external genitalia differentiated, fingers and toes clearly marked out. Fine downy hair appears in the fourth month, when the foetus is 8 inches long ; in the fifth, foetal movements begin and the skin becomes covered with a thick greasy layer of secretion. By the seventh month, the eyelids have opened and the testicles descended into the scrotum ; and, though the foetus may now be viable, or capable of living, if prematurely born, it is not adequately clothed with subcutaneous fat until the end of the ninth month.

At *birth*, the uterus contracts, rupturing the membranes and expelling first the foetus and amniotic fluid,

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then the placenta, and finally the membranes like an umbrella turned inside out. Certain important changes take place in the child at or soon after this moment. During foetal life the lungs have remained unexpanded and airless; they need no blood and the stream in the pulmonary artery is shunted through a bypass directly into the aorta. With the first cry, the lungs expand, the pulmonary circulation is established, and the pulmonary-aortic channel soon closes off. The parts of the umbilical vessels contained within the child also shrivel up and obliterate. Thus the former parasite has become an independent organism.

The Breasts and Milk. The breasts or mammary glands are accessories of the reproductive system; designed for milk production, they are however present in rudimentary form in the male as well as the female. In the female, they form rounded eminences, small before puberty, between the skin and underlying muscle on the front of the chest. At puberty they develop rapidly with the uterus; they enlarge further in pregnancy and especially in the lactation period after delivery; and in old age they atrophy. There are minor cyclical changes of congestion with menstruation.

Each breast is divided into numerous lobes; and each lobe contains a branched secreting system of gland spaces, supported by pervading fatty tissue; and the ducts of these structures converge as 15–20 main milk channels, to open at the summit of the nipple.

The breasts develop throughout pregnancy in preparation for lactation. The first few days after delivery of the child they yield only a watery fluid or colostrum containing a few fat globules; only after this does milk secretion begin properly. The adequate secretion of milk is governed by the hormones of pituitary and ovaries, and there is also a reciprocal relation between lactation and menstruation ; resumption of the monthly periods after delivery of the child may be long delayed by continued suckling. In addition, the child's sucking at the breast is a powerful stimulus to the proper contraction or involution of the uterus after childbirth, and is therefore of the greatest importance to the mother herself.

The milk of all mammals is essentially similar, a slightly acid fluid, opaque from the presence of myriads of finely dispersed fat globules. Its main constituents are : (i) *protein* (caseinogen) which is converted into a solid casein clot or curd in the stomach, or when it is allowed to sour ; from this can be expressed a liquid whey ; (ii) *sugar* (lactose) ; (iii) *fat.*

In man, these are found in the proportions of protein 1·5 per cent, lactose 6·5 per cent, and fat 3·5 per cent ; and cows' milk differs in that it contains more protein and less sugar, the fat content being much the same. If therefore it is necessary to use it for infant feeding, it can be made approximately the same in composition as human milk by adding water to dilute the protein content and making up the sugar ; but it is very much a second-best substitute, and the physical benefits natural feeding confers on both mother and child, as well as the inestimable but profound psychological advantages, should make breast feeding always the method of choice.

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